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ON YUGOSLAVIAN (BALKAN) TICKS [IXODOIDEA]

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(With 2 Figures in the Text)

CONTENTS

		PAGE
I.	Geographical and historical notes	271
II.	Classification of Yugoslavian ticks	272
III.	Seasonal occurrence of Yugoslavian ticks	276
IV.	Distribution of Yugoslavian ticks	277
V.	Economic and veterinary importance of Yugoslavian ticks. Tick paralysis	279
	References	280

I. GEOGRAPHICAL AND HISTORICAL NOTES

THE state of Yugoslavia provides both an abundant and important source for zoological studies owing to its varied geographical, climatic and ethnographic conditions. To the student of ticks especially there is hardly a country in Europe which offers as large a field for study as Yugoslavia. Therefore I trust a short description of the Yugoslavian ticks and their biological habits, so far as known, will be of some interest.

In virtue of its geographical configuration, Yugoslavia comprises five regions, each of which possesses its particular climatic conditions:

(1) Slovenia, with a highly humid alpine climate, characterized by a short cool summer and a long and severe winter, separated by a short spring and autumn; (2) the steppe region, north of the rivers Drava and Danube, with a moderately humid climate, a short hot summer and a long severe winter; (3) a central continental area, comprising Croatia, Old Serbia, Bosnia, etc., with fairly even seasons, humid at all times, with a hot summer and a severe winter; (4) the Adriatic coastal region (Dalmatia) with a Mediterranean type of climate, a long hot summer, a short mild winter, short spring and autumn, with a heavy rainfall during the cooler season; (5) the Aegean region (the R. Vardar valley in southern Serbia) with a long subtropical summer and a short but severe winter, a short spring and autumn, and moderate humidity in the cooler season.

Except for the region of the "karst" along the Adriatic coast the whole country is covered by an abundant vegetation of every kind. The whole country south of the rivers Sava and Danube is mountainous. Northwards opens the great Pannonian plain. Agriculture and stock-breeding are the chief occupation of the people. While the northern parts are inhabited by more advanced people, the southern regions are still occupied by more or less primitive peasants, though progress is everywhere going on. Thus, both

because of the above climatic conditions in southern Serbia, and because it was for centuries a conjunction of various races and nations, there is no reason for surprise at the abundance of ticks.

The study of the ticks occurring on the territories which nowadays form Yugoslavia was commenced by several authors both before and during the Great War. Berlese, Canestrini & Neumann give reports of *Haemaphysalis cinnabarina punctata* found in Croatia and Dalmatia (12).[1] Neumann also recorded *Rhipicephalus bursa* from Croatia and Dalmatia, and *Hyalomma aegyptium* (11) (not *H. syriacum*!) in Herzegovina. A great deal was done during the Great War, in southern Serbia, by Schulze, to whom the creation of new names for species as *Hyalomma scupense*, *H. detritum dardanicum*, *Haemaphysalis otophila*, and *Ixodes hexagonus dardanicus* (5, 18) is due. Similarly, after the Great War, Minning described *Boophilus calcaratus* and *B. schulzei* from southern Serbia (7). It was not until 1926 that the study of Yugoslavian ticks was undertaken by local workers, first of all by Repić, obviously influenced by Schulze (17). Then followed Apfelbeck (1), Babić (2), Mlinac & Oswald (8, 9), and Oswald (14, 15, 16). Prior to 1935, these authors merely recorded the occurrence of species already mentioned in Schulze's list. In 1935, Mlinac & Oswald diagnosed tick paralysis (8) as causing heavy losses in ruminants in southern Serbia, which disease, in addition to both piroplasmosis and fowl spirochaetosis, afforded a sufficient reason for a systematic investigation of Yugoslavian ticks, not only of their classification but also of their biological characteristics. Since then I have had occasion to extend Schulze's list of the southern Serbian ticks with the following names: *Ixodes canisuga*, *I. ricinus* var. *scapularis*, *I. hexagonus* var. *cookei*, *I. brunneus*, *Hyalomma aegyptium* (*syriacum*), *Haemaphysalis cholodkovskyi* (*H. cinnabarina punctata* var. *longicornis*), *H. cinnabarina punctata* var. *recta*, *H. concinna*, *H. leachi media*, *H. sulcata*, *Dermacentor cruentus*, and *Boophilus schulzei*.

I have also examined several bats and their habitats (caves) for both *Ixodes vespertilionis* and *Argas vespertilionis*, as well as some pigeon coops for *Argas reflexus*, but so far without success.

II. Classification of Yugoslavian ticks

The following is a complete list of the species of ticks at present recorded as occurring in Yugoslavia:

(1) *Ixodes ricinus* (Linnaeus, 1746, 1758) (11, 12).
(2) *I. ricinus* var. *scapularis* (Say, 1821) (12).
I. scapularis Say, 1821 (11).
(3) *I. hexagonus* Leach, 1815 (12).
I. hexagonus hexagonus Leach, 1815 (11).
(4) I. *hexagonus* var. *cookei* (Packard, 1869) (12).
I. cookei Pack, 1869 (11).

[1] To avoid confusion and numerous repetitions the references in the text are marked by numbers in brackets.

(5) *I. canisuga* Johnston, 1849 (12).
I. hexagonus inchoatus Neum. 1901 (11).
(6) *I. brunneus* Koch, 1844 (12).
I. frontalis frontalis Panz. 1798 (11).
(7) *Hyalomma scupense* Schulze, 1918 (5, 18).
(8) *H. detritum dardanicum* Schulze & Schlottke, 1929 (18).
(9) *H. aegyptium* (Schulze, 1929) (18).
H. syriacum Koch, 1844 (11).
(10) *Dermacentor reticulatus reticulatus* Fabricius, 1794 (11).
D. niveus (Olenev, 1928) (13).
(11) *D. cruentus* Koch, 1844 (11).
(12) *Haemaphysalis inermis* Birula, 1895 (11, 12).
(13) *H. cinnabarina* var. *punctata* (Canestrini & Fanzago, 1877) (12).
H. punctata punctata Can. & Fanz. 1877 (11).
(14) *H. cholodkovskyi* Olenev, 1928 (cit. (4)).
H. cinnabarina var. *cretica* Senevet & Caminopetros, 1936 (4).
H. cinnabarina punctata var. *longicornis* Oswald, 1937 (14).
(15) *H. cinnabarina punctata* var. *recta*, n.var.
(16) *H. concinna* Koch, 1844 (11, 12).
(17) *H. leachi media*, n.subsp.
(18) *H. sulcata* Can. & Fanz. 1877 (11).
(19) *Rhipicephalus bursa* Can. & Fanz. 1877 (11).
(20) *R. sanguineus sanguineus* Latr. 1806 (11).
(21) *Boophilus calcaratus balcanicus* Minning, 1935 (7).
? *Margaropus calcaratus calcaratus* Birula, 1880 (11).
(22) *B. schulzei* Minning, 1935 (7).
(23) *Argas persicus* Oken, 1818 (12).
A. persicus persicus Fisch.-Waldh. 1823 (11).

For the names of the hosts on which the above-mentioned species of ticks were found, see Table I.

(2) *Ixodes ricinus* var. *scapularis*

Nuttall *et al.* (12) say: "...The form is certainly very near *I. ricinus*, and if found in Europe would be attributed to that species with little hesitation....It seems to us impossible to accord it higher rank than that of a variety of *I. ricinus*...." I find the European (Yugoslavian) type identical with the American one, and, therefore, I have no reason to create a new name for it.

(4) *Ixodes hexagonus* var. *cookei*

Nuttall *et al.* (12) say: "...Evidently the N. American form of *I. hexagonus*." I consider the European (Yugoslavian) type identical with the American, and there is, therefore, no reason to create a new name.

Table I

Species	Stage	Host
Ixodes ricinus s.str.	L	*Lacerta agilis, L. muralis, L. viridis, Erinaceus europaeus, Sciurus vulgaris*
	o	*Lacerta agilis, L. muralis, L. viridis, Erinaceus europaeus, Sciurus vulgaris, Lepus europaeus*
	♀♂	*Equus caballus, E. asinus, Bos taurus, Ovis aries, Capra hircus, Sus scrofa domesticus, Canis familiaris, Felis domestica, Homo sapiens, Rupicapra rupicapra, Lepus europaeus, Sciurus vulgaris, Erinaceus europaeus*
I. ricinus var. *scapularis*	♀	*Bos taurus, Ovis aries, Capra hircus*
I. hexagonus s.str.	♀	*Bos taurus, Ovis aries, Capra hircus, Sus scrofa domesticus, Canis familiaris, C. vulpes*
I. hexagonus var. *cookei*	♀	*Bos taurus, Ovis aries, Capra hircus*
I. canisuga	♀♂	*Canis familiaris, C. vulpes, C. aureus*
I. brunneus	o♀	*Crex crex, Garrulus glandarius, Turdus merula, T. philomelos, Aquila chrysaëtos*
Hyalomma scupense	L	*Lacerta muralis, L. viridis, Crex crex, Garrulus glandarius, Turdus philomelos, Passer montanus*
	o	*Lacerta muralis, L. viridis, Crex crex, Garrulus glandarius, Turdus merula, T. philomelos, Upupa epops, Aquila chrysaëtos, Gallus domesticus Canis familiaris, Lepus europaeus*
	♀♂	*Equus caballus, E. asinus, Bos taurus, Ovis aries, Capra hircus, Bubalus domesticus, Sus scrofa domesticus, Homo sapiens*
H. detritum	Lo♀♂	As in *scupense*
H. aegyptium	o♀	*Testudo graeca*
Dermacentor niveus	♀♂	*Equus caballus, Bos taurus, Ovis aries, Capra hircus, Sus scrofa domesticus*
D. cruentus	♀	*Bos taurus, Ovis aries*
Haemaphysalis inermis	o	*Lacerta muralis, L. viridis*
	♀♂	*Bos taurus, Ovis aries, Capra hircus*
H. cinnabarina punctata s.str.	L	*Lacerta muralis, L. viridis, Turdus philomelos, Gyps fulvus, Aquila chrysaëtos, Alectoris graeca*
	o	*Lacerta muralis, L. viridis, Vipera ammodytes, Crex crex, Turdus merula, Alectoris graeca, Gallus domesticus, Sciurus vulgaris, Erinaceus europaeus, Lepus europaeus*
	♀♂	*Equus caballus, Bos taurus, Ovis aries, Capra hircus, Canis familiaris, Homo sapiens, Sus scrofa domesticus*
H. cinnabarina punctata var. *recta*	♂	*Bos taurus, Ovis aries, Capra hircus*
H. cholodkovskyi	Lo♀♂	As in *H. cinnabarina punctata* s.str.
H. concinna	♀	*Ovis aries*
H. leachi media	♀♂	*Canis familiaris, C. vulpes*
H. sulcata	o	*Lacerta viridis*
Rhipicephalus bursa	♀♂	*Equus caballus, Bos taurus, Ovis aries, Capra hircus, Canis familiaris, Homo sapiens*
R. sanguineus	o	*Lepus europaeus, Erinaceus europaeus, Canis familiaris*
	♀♂	As in *R. bursa*, and *Erinaceus europaeus*
Boophilus calcaratus	o♀♂	*Equus caballus, Bos taurus, Ovis aries, Capra hircus*
B. schulzei	♀	*Bos taurus*
Argas persicus	Lo♀♂	*Gallus domesticus, Anser domesticus, Anas boschas domestica, Aquila chrysaëtos, Homo sapiens*

(7, 8) *Hyalomma scupense, H. detritum*[1]

The male of *scupense* is clumsier than *detritum*. Also the former has a shorter tarsus IV than the latter. The female of *scupense* is characterized by having a roundish heart-shaped scutum, broadest in the middle. The female of *detritum* has a scutum longer than broad, broadest behind the eyes. Tarsus IV of *scupense* tapers abruptly, while that of *detritum* is rounded at its end. The scutal punctation in the males and females of both types varies from fine to coarse.

A sharp differentiation between the two types is often impossible; intermediate forms are not uncommon.

(14) *Haemaphysalis cholodkovskyi*

The male of *cholodkovskyi* has a long spur on coxa IV (4), curved outwardly, not inwardly as in *cinnabarina punctata*. The former has nine festoons only, not eleven as found in the latter. There is a dorsal, retrograde spur on article 2 of the palp in both males and females of *cholodkovskyi*. The spurs in the female of *cholodkovskyi* are short so that the coxae are practically unarmed. The male has very long cornua, and, therefore, I have considered this tick for years as a long-horned variety of *cinnabarina*, and classified it as *Haemaphysalis cinnabarina punctata* var. *longicornis*, 1937 (14).

(15) *Haemaphysalis cinnabarina punctata* var. *recta*, n.var.

Recently I found males of *cinnabarina punctata* on domestic ruminants with a long, straight spur on coxa IV, curved neither inwardly as in *cinnabarina punctata* s.str., nor outwardly as in *cholodkovskyi*. The cornua are stronger than in *cinnabarina punctata*. Punctations and festoons as in *cinnabarina punctata*. I therefore consider *recta* as a variety of *cinnabarina punctata* s.str. Can. & Fanz.

(17) *Haemaphysalis leachi media*, n.subsp.

During the past three years I have found examples of *leachi* on carnivores which seemed to be intermediate forms between *leachi* s.str. and *numidiana*. Both males and females are characterized by having slighter spurs on palpal article 2 than those found in *leachi* s.str., but far stronger than those of *numidiana*. I have, of course, compared specimens of *leachi* s.str. with *leachi media* of the same size. I therefore consider *media* as a subspecies of *leachi* s.str. Audouin. I have never found *leachi* s.str. in Yugoslavia.

(18) *Haemaphysalis sulcata*

Nuttall *et al.* (12), and Neumann (11) consider it to be the nymph of *cinnabarina punctata*. Recently, Matikašvili (6) has again reported the occurrence of *sulcata* on lizards in Grusia, Russia. I would draw attention to the fact that the normal nymph of *cinnabarina punctata* has an elongate-oval

[1] Most authorities would consider both to be merely subspecies or varieties of *Hyalomma aegyptium*, ED.

scutum, while by *sulcata* I understand a nymph of *Haemaphysalis* with a round scutum, collected from lizards in Yugoslavia. Thus *sulcata* resembles the nymph of *concinna* to a certain degree.

Schulze in 1918 (5) describes a male of a species of *Haemaphysalis* with a reduced spur on coxa IV, found on horses in southern Serbia, and gives it the specific name *otophila*. I have never found such a tick, but would draw attention to Dschunkowsky's tick, described by Nuttall & Warburton as the Transcaucasian variety of *cinnabarina punctata* (12).

(22) *Boophilus calcaratus, B. schulzei*

I find the males of the two varieties practically indistinguishable. The female of *calcaratus balcanicus* has the scutum rounded in front of the eyes, while in *schulzei* it is angular in front of the eyes. Differentiation between the two forms is often uncertain as intermediate forms are not seldom found.

III. Seasonal occurrence of Yugoslavian ticks

As a result of observations covering a period of three years I have come to the conclusion that the majority of Yugoslavian ticks are characterized by a strict seasonal occurrence of adults on the host, at least it seems to be so with the ticks in the Vardar valley in southern Serbia. There are species which occur once a year on host as adults, viz. *Hyalomma scupense*, *H. detritum*, *Rhipicephalus bursa* and *Boophilus calcaratus* including *schulzei*. Other species appear as adults on the host twice a year, viz. *Ixodes ricinus*, *I. hexagonus*, *Haemaphysalis cinnabarina punctata*, *H. cholodkovskyi*, *H. inermis* and, probably, *H. concinna*, disappearing at the beginning of summer and reappearing towards its end, their seasons being spring and autumn. On the approach of winter the species of both groups usually hibernate off the host, except for *Boophilus* being a one-host tick, thus continuing their life cycle.

Fig. 1 represents approximately the seasonal prevalence in southern Serbia (particularly the Vardar valley) of the various species found on domestic animals throughout the period from March to December inclusive. The relative intensity of infestation by each species was estimated from the number of examples of each collected. In the remaining regions of the country, excepting the Adriatic coast, where the circumstances fairly resemble those of the valley of the Vardar, such remarkable seasonal occurrence seems to be far less expressed, obviously on account of both the reduced number of species and the different climatic conditions. The seasonal distribution in the valley of the Vardar can easily be explained by the climatic conditions prevailing in that region. The first group comprises species that prefer a hot and arid summer, but which are also adaptable to two temperatures and high humidity. The second group is represented by species that cannot endure such a summer; they find their favourable environmental factors during the two mild and humid seasons, i.e. spring and autumn.

With respect to the occurrence of the immature stages of species from both groups on wild mammals, birds and reptiles, a certain regularity seems also to

obtain, but I prefer to defer consideration of this subject until I have collected more information.

IV. Distribution of Yugoslavian ticks

It is certain that the whole of Yugoslavia is invaded by ticks, but there is a great difference between the northern and southern areas, divided by the rivers Sava and Danube, in respect both to quality and quantity of invasion. While

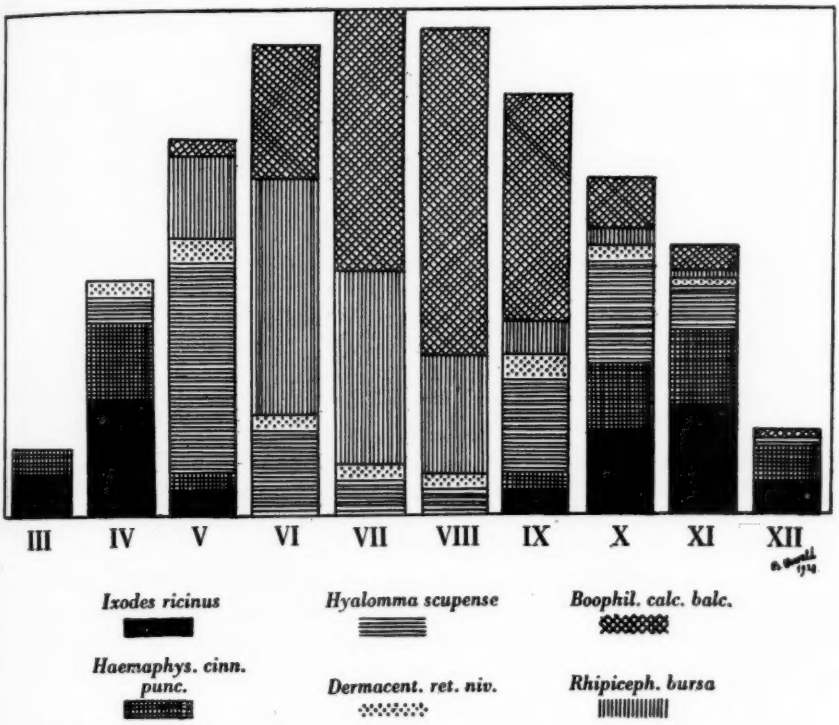

Fig. 1. Diagram representing the seasonal distribution and incidence of the commoner species of Yugoslavian ticks.

in the north only a few species and light infestation are met with, in the south, especially in the valley of the Vardar and along the Adriatic coast, we find a rich natural collection causing heavy infestations on domestic animals.

In the north occur species that prefer a mild, humid environment, e.g. *Ixodes*, *Haemaphysalis* and *Dermacentor* to a certain degree, while in the south every Yugoslavian species is found, in accordance with a more or less expressed seasonal distribution.

In Fig. 2 I have attempted to furnish the reader with a distribution map, based on my observations up to the present, but possibly subject to slight alteration as more information becomes available.

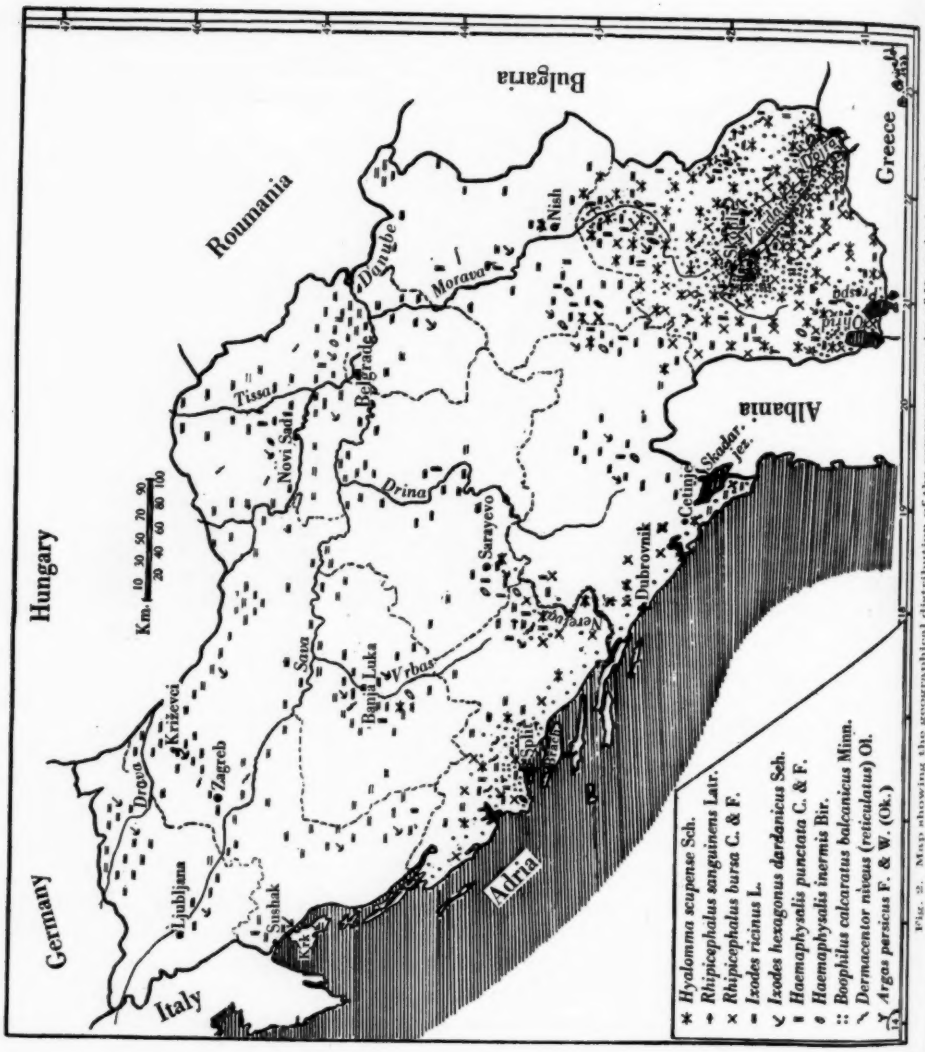

Fig. 2. Map showing the geographical distribution of the commoner species of Yugoslavian ticks.

The heavy tick infestation found in certain southern regions, especially in the valley of the Vardar, can be attributed to both favourable climatic conditions and the primitive state of agriculture and livestock breeding.

V. Economic and veterinary importance of Yugoslavian ticks

In the list of causes of severe losses due to various contagious diseases, such as swine fever, anthrax, glanders, rabies, and fowl cholera, by internal parasitic infestations, such as liver fluke, echinococcosis, strongylosis and mange, tick-transmitted diseases figure prominently in Yugoslavia.

Both *babesiellosis* and *theileriosis* in cattle, horses and sheep, and *spirochaetosis* and *balfouriosis* in poultry, are causes of severe mortality in livestock throughout Yugoslavia, more especially in the south. Recently *tick paralysis* (8) in ruminants and *anaplasmosis* in cattle (10) have been identified in southern Yugoslavia.

Tick paralysis

Tick paralysis in Yugoslavia appears worth a few lines of discussion. The disease is known by several local names, of which (though it means nothing) "*Shimteera*" has been officially accepted. It was first recorded in the autumn of 1935 in southern Serbia, as having occurred in ruminants, goats, sheep and calves. The illness sets in suddenly, with a staggering gait, tumbling and falling. Affected animals are unable to rise without assistance. Symptoms of dyspnoea, diminished rumination and difficulties in taking food, soon follow. By the third or fourth day the animals die, unless spontaneous recovery takes place. In some animals severe eye-affections and nasal discharge have been observed. The temperature remains nearly normal. The autopsy gives negative results, though a slight oedema of the lungs is sometimes met with. Removal of the ticks by hand picking leads to an early recovery. Attempts to transmit the disease to healthy animals by inoculation of blood obtained from affected ones have been unsuccessful. No causal organism could be isolated from the material obtained from animals that had died.

It is a matter of special interest that the "*Shimteera-disease*" is believed to recur at regular, mostly three-yearly intervals. No wonder that I have impatiently expected the next return of the disease which actually took place this autumn (1938), just in the same districts as three years ago! Thanks to the attention of the district veterinarians, I am now in possession of the ticks obviously involved in the disease. Unfortunately, not only one, but several species have been collected from affected animals, as follows: (1) *Ixodes ricinus* s.str., (2) *I. ricinus scapularis*, (3) *I. hexagonus* s.str., (4) *I. hexagonus cookei*, (5) *Haemaphysalis cinnabarina punctata* s.str., (6) *H. cinnabarina punctata recta*, (7) *H. cholodkovskyi*, (8) *H. inermis*, and (9) *H. concinna*.

Each affected animal was invaded by at least two of the above species, therefore future experiments will have to decide which of them is the real vector. All that I can say at present is that *tick paralysis* in Yugoslavia un-

Fig. 2. Map showing the geographical distribution of the commoner species of Yugoslavian ticks.

doubtedly appears to be in causal relationship with the seasonal occurrence of the autumnal species of ticks, and that the popular opinion as to the triennial recurrence of the disease is correct. I am unable to correlate the triennial recurrence of the disease with the annual occurrence of the tick!

It should be mentioned that, in the course of biological researches on Yugoslavian ticks, it has been shown (9) that the eggs of *Hyalomma scupense*, *Boophilus calcaratus* (16), *Rhipicephalus bursa* and *R. sanguineus* contain a toxin which, when administered subcutaneously to guinea-pigs, provokes a fatal paralysis. An extract made from about 0·1 g. weight of eggs is sufficient to cause death within 4–6 days. It remains, however, an open question whether this toxin is that which is responsible for the causation of natural tick paralysis of ruminants.

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THE COCCIDIA INFESTING THE COTTONTAIL RABBIT, *SYLVILAGUS NUTTALLII GRANGERI* (ALLEN), WITH DESCRIPTIONS OF TWO NEW SPECIES

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(With 3 Figures in the Text)

The oocysts studied were concentrated from the contents of the colon and caecum of the cottontail rabbit. The concentration method of Benbrook (1929) has been found to serve best.

Sporulation was induced in 2 % dichromate solution. The depth of the cultures was between 3 and 4 mm. The cultures were kept at room temperature. In general the minimum sporulation time was slightly greater than that usually given for known species.

Becker (1934) says that none of the known species of coccidia infesting the rabbit is capable of developing to maturity in sheep or cattle; however, *Eimeria environ* n.sp. is morphologically indistinguishable from *Eimeria aemula* Yakimoff of the sheep.

In several species of coccidia the presence or absence of an extra-residual body is a constant morphological characteristic.

Species of coccidia infesting the cottontail rabbit

Eimeria stiedae Lindeman

Only occasionally is this species found to infest the cottontail rabbit. The morphology and the lesions produced are similar to those described for the domesticated rabbit.

Variety of **Eimeria media** Kessel 1929

The colourless elliptical oocysts of this variety measure 24·07–33·20 μ by 17·01–23·65 μ, average 28·24 by 19·61 μ. The length/breadth ratio is 1·44. A micropyle is visible in the lateral circular thickening of the oocystic wall. The circular thickening imparts a truncate appearance to the oocyst. The ovoid residual body averages 5·14 μ in diameter. The sporoblasts measure 10·29–16·6 μ by 6·64–9·96 μ, average 13·74 by 7·55 μ. An intra-residual body was not discernible. Minimum sporulation time was about 45 hr.; the majority required 70 hr.

Comparative Characters of Rabbit Eimeria

(All measurements are in microns)

All measurements, except those for variety *E. media, environ* and *maior*, are taken from Becker (1934)

	E. stiedae	*E. irresidua*	*E. environ*	*E. perforans*	*E. magna*	*E. media*	*E. media* variety	*E. maior*	*E. leporis*
					Oocyst				
Length:									
Variation	28–40	31–43	21–29·88	15–30	28–40	27–36	24–33·2	41–51·46	26–38
Average	37·5	38·3	26·27	25·5 (22·7)	35	31·2	28·24	46·52	32
Breadth:									
Variation	16–25	22–27	16–23·24	11–20	20–26	15–22	17–23·65	26–36·52	13–20
Average	21·5	25·6	20·51	15·5 (14·2)	24	18·5	19·61	30·91	16
Length/ breadth ratio	1·85	1·50	1·30	1·59	1·47	1·69	1·44	1·50	2
Colour	In the liver colourless to light pink, in the intestine reddish orange	Light yellow, some darker	Colourless, a few greenish to straw	Colourless, a few show a tinge of pink	Flesh or brownish yellow	Pink to a dark orange pink	Colourless	Brownish yellow	Almost colourless
Sporulation time (hr.):									
Minimum	58	50	50	30	48	40	45	50	—
Majority	70	64	68–70	46	60	52	70	80	—
Micropyle	Visible	Visible	Usually not visible	Not visible	Visible	Visible, convex	Visible, convex	Visible	Not visible
Extra-residual body	None	None	None	3·2	9·6	5·2	5·14	6·1	Yes
					Sporocyst				
Av. length	18	—	12–17·84 15·57	—	—	—	10–16·6 13·74	18–24·9 21·24	—
Av. breadth	10	—	7–9·54 8·28	—	—	—	6–9·96 7·55	8–11·62 10·37	—

Wenyon (1926) pictures an oocyst with a circular thickening of the wall about the micropyle. This oocyst he has labelled *Eimeria stiedae*. Kessel & Jankiewicz (1931) have shown this to be in error. Until further studies of the coccidia of wild rabbits and hares are made, it would seem best to consider this form a variety of *E. media*.

1 2 3

Fig. 1. *Eimeria environ*. ×1200.
Fig. 2. *Eimeria maior*. ×1200.
Fig. 3. Variety *Eimeria media*. ×1200.

Eimeria maior n.sp.

The oval oocysts of this species can readily be distinguished by their colour and size. The colour is a constant yellowish brown. The oocyst wall is of two parts. The outer envelope contains the pigment. In many of the oocysts this envelope appears to be pectinate. It is of uneven thickness, being thinnest opposite the micropyle and thickest near the edge of the micropyle.

The oocysts measure 44–51·46 μ by 26–36·52 μ, average 46·52 by 30·91 μ. Length/breadth ratio equals 1·50. The micropyle is visible as a thinning and slight indentation of the oocystic wall.

An extra-residual body is present. It is variable in size and shape; on two occasions it was seen to be dispersed. The commonest spherical form averaged 6·1 μ in diameter.

The sporoblasts measured 18–24·9 μ by 8–11·62 μ, average 21·24 by 10·37 μ. An intra-residual body was clearly visible.

Minimum sporulation time was 50 hr.; majority, 80 hr.

Eimeria environ n.sp.

The ovoid oocysts measure 21·58–29·88 μ by 16·18–23·24 μ, average 26·76 by 20·51 μ. The length/breadth ratio is 1·30. Most of the oocysts are colourless but occasionally one of a greenish or straw tinge is found. The micropyle may

or may not be visible. When visible it appears to possess a cap which slightly protrudes beyond the curvature of the oocystic wall. There is no extra-residual body. The sporoblasts measure 12·45–17·84 μ by 7·05–9·54 μ, average 15·57 by 8·28 μ. No intra-residual body was discernible. The minimum sporulation time was 50 hr.; the majority, 68–70 hr.

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ON FOUR NEW SPECIES OF CERCARIAE. A CONTRIBUTION TO SEWELL'S EVOLUTIONARY SCHEME

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(With 9 Figures in the Text)

Introduction

One of the commonest species of snails available in Northern India is *Indoplanorbis exustus* (Deshayes), a species which is the most frequently infected with a large number of forms of cercariae. The present work deals with four new species of cercariae that have as their primary host the above-mentioned mollusc. Of these four species two, belonging to the group Xiphidiocercariae, have been named *Cercaria lühei* and *C. gopyjungi*, while the other two, belonging to the furcocercous group, have been named *C. ajmeri* and *C. anasagari* respectively.

Material and methods

The material of *C. lühei* was collected from the ponds of Allahabad, U.P., and that of *C. gopyjungi* from the Gopyjung pond, a village about 100 miles from Allahabad. The furcocercous cercariae material was collected from the Anasagar Tank, Ajmer (Rajputana). Examination of the snails was carried on from time to time, and study of the cercariae was made after emergence from the host. Detailed studies of all these forms have been made on living material with the aid of an oil-immersion lens. Observations were made on the living cercariae under uniform pressure of the cover-slip and when the activity of the animal had ceased. Measurements were made of living material, and represent the averages of at least a dozen different individuals. Neutral red was used throughout my work for the examination of living specimens with great satisfaction. Entire mounts were stained with borax carmine and Delafield's haematoxylin. Sketches were made by a camera lucida.

Cercaria lühei n.sp. (Figs. 1, 2).

The specimens were collected from a number of snails during the first week in August 1935, and infection was about 50 %. The infection gradually increased, reaching 95 % at about the end of the month and declined towards the first week of September. The corroded, thin, weak and enlarged shell of the host and the deep orange red colour of the sporocysts, as seen through it, betray the infected snail.

Average dimensions in mm.: body length 0·177; body breadth 0·085; tail length 0·13; tail breadth 0·014; oral sucker 0·042 × 0·04; acetabulum 0·042 × 0·046; stylet 0·018 × 0·003; sporocyst 1·08 × 0·162.

The cercariae are not very active. On the flat surface they progress in the usual leech-like motion by the alternate use of their suckers. The body is capable of altering its form enormously. Like other Xiphidiocercariae they contract the body while swimming and whip the water in all directions with the tail.

The body is broadest at the acetabular level, and from this point it tapers towards both ends. The whole of the surface is covered with transverse rows of backwardly directed, equal-sized spines. Beneath the cuticle numerous cystogeneous cells, containing a granular material, are scattered, covering mainly the posterior two-thirds of the body. They form irregular rows on each side of the body, and are specially numerous on the dorsal surface. The anterior conical end is occupied by the more or less oval oral sucker, the dorsal wall of which is armed with the stylet. The stylet is approximately six times as long as broad and with a thickening about one-third from its anterior end. The acetabulum is circular, very powerful and projects slightly ventrally, but, unlike *C. indica* XVII (Sewell, 1922), is not armed with spines. It is larger than the oral sucker and is placed just behind the middle of the body length. The postero-ventral angles of the body are produced in a pair of lappets, which lie on either side of the base of the tail, enclosing it in a groove. The inner walls of these lappets are thick and refractile, bearing long needle-like spines pointing towards the acetabulum. The caudal pockets are well developed.

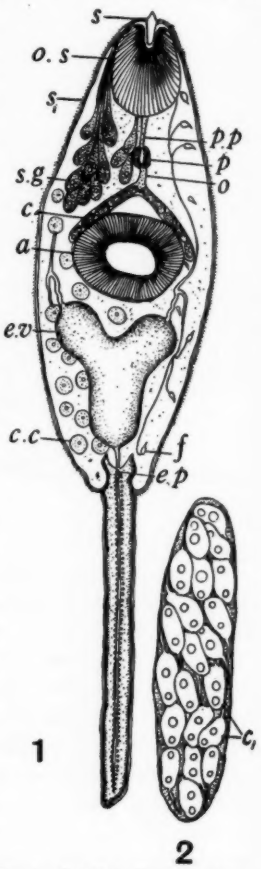

Fig. 1. *C. lühei*. Ventral view. × 200.

Fig. 2. *C. lühei*. Sporocyst. × 40.

The mouth leads into the cavity of the oral sucker, behind which follows a long prepharynx and a muscular oblong pharynx. The oesophagus is short and the intestinal caeca branch off almost immediately, reaching back to about one-third the acetabular length. In *C. indica* XVII (Sewell) they reach to the level of the posterior margin of the acetabulum. The salivary gland cells which lie on either side of the body between the pharynx and the acetabulum are composed of many pyriform cells with granular protoplasm and small rounded nuclei. The ducts of these cells open on the anterior lip of the mouth.

The excretory bladder is Y-shaped, muscular and large. From the rounded

tips of each horn the main excretory tubes arise. These take a convoluted course forwards to the level of the post-acetabular margin where each divides into two collecting tubes. The anterior tubes run forward, and in the vicinity of the oral sucker divide into three branches, each tipped with a flame cell. In the region between the acetabulum and the horns of the bladder are seen three other flame cells. I have not been able to trace their connexions, but judging from their position they would probably join the descending tube. The flame cell formula is probably $2 \times 3 \times 3 = 18$ flame cells. A caudal canal is given off from the posterior end of the bladder and runs to the tail. The excretory pore lies at the junction of the tail and the body.

I have not been able to detect any trace of the genital system.

Development takes place in reddish brown sporocysts, which are attached by one end to the infected liver mass. These are long cylindrical structures with tapering rounded ends and are dotted with the liver tissue. The free end is capable of performing spontaneous movements. Sporocysts appear to be of two sizes. The smaller ones are oval and sac-like, the longer ones are cylindrical. Each sporocyst contains a large number of cercariae in the same stage of development.

Cercaria gopyjungi n.sp. (Figs. 3–5).

The specimens were collected at Gopyjung. Average dimensions in mm.: length of body 0·289; breadth of body 0·071; tail length 0·187; tail breadth 0·02; oral sucker $0{\cdot}054 \times 0{\cdot}034$; acetabulum $0{\cdot}051 \times 0{\cdot}051$; stylet $0{\cdot}020 \times 0{\cdot}003$; pharynx $0{\cdot}015 \times 0{\cdot}009$; sporocyst $1{\cdot}62 \times 0{\cdot}18$.

These cercariae are larger than *C. lühei*. On the flat surface they move in the usual leech-like motion, but they are much more active than *C. lühei*. They prefer to move laterally and in this condition the acetabulum protrudes considerably. Like other Xiphidiocercariae they contract the body while swimming and whip the water in all directions with the tail. They are present in large numbers, and infection was about 6 % in the snails collected. The stylet is long and pointed, having no thickening. The body is broadest at the level of the acetabulum and tapers towards both ends, but more towards the anterior end. The whole body is covered with backwardly directed transverse rows of spines. The postero-ventral margin is curved in to form a lappet on either side. The inner walls of these are thick and refractile, carrying long acicular spines. These are facing the acetabulum and are exactly like those in *C. lühei*. These enlarged spines probably help the animal during decaudation. When the animal turns its ventral side upwards these spine-bearing laminae of the two sides are seen to resemble a pair of pincers. The same appearance is given by *C. lühei* in the ventral position. Cystogeneous cells are numerous and scattered over the posterior two-thirds of the body, but more particularly, though irregularly, along the lateral sides, as in *C. lühei* or *C. indica* XVII (Sewell). They are more numerous dorsally and cover the whole surface. The anterior

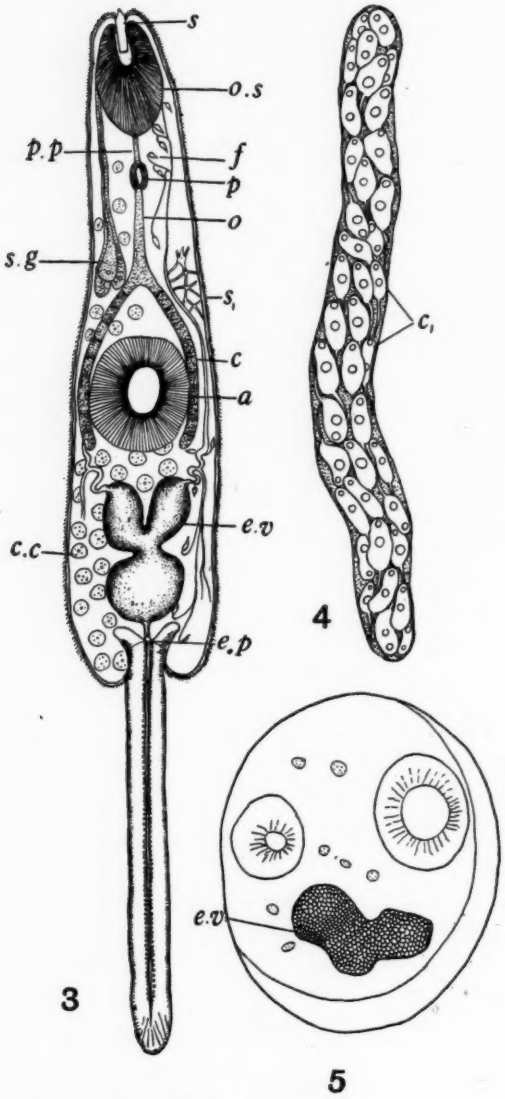

Fig. 3. *C. gopyjungi*. Ventral view. ×200.
Fig. 4. *C. gopyjungi*. Sporocyst. ×40.
Fig. 5. *C. gopyjungi*. Cyst showing excretory vesicle with granules. ×200.

end is rounded and is occupied by the oral sucker, the dorsal wall of which is armed with the stylet.

The mouth lies in a cleft, a little behind the terminal end. The oral sucker is connected by a long prepharynx to a comparatively short muscular pharynx, and then follows a long oesophagus, and, finally, the intestinal caeca, which reach the posterior margin of the acetabulum. The salivary gland cells lie three on each side of the body, reaching the anterior margin of the acetabulum. They are large and granular with rounded nuclei and pour their contents by their long ducts on to the anterior lip of the mouth. The powerful acetabulum is situated more posteriorly in the body than that of *C. lühei*.

From the tips of the horns of the bladder arise the main excretory tubes which divide into anterior and posterior branches before reaching the posterior margin of the acetabulum. The ascending branches divide into a network of finer branches just above the acetabular region. Anteriorly, however, I have seen six flame cells on each side as indicated in the figure. The posterior branches also give off tubules along their course, but I have seen only six flame cells on either side. Half of them show their connexions to the descending branches; the rest do not, but from their position it is evident that they also join the posterior branches. Hence the flame cell formula is: $2 \times 4 \times 3 = 24$ flame cells. There is also a caudal canal going to the tail. The excretory pore lies at the junction of the tail and the body. The excretory product is dark and refractile.

I have not seen any trace of the germ cells.

Development takes place in reddish brown sporocysts. These are long cylindrical structures, each containing cercariae in the same stage of development. They do not exhibit any spontaneous motion, as is the case in *C. indica* XVII (Sewell) and *C. lühei*. The infection of the liver mass is along definite lines and is not so severe as *C. lühei*. In both *C. lühei* and the present form I have come across cysts in the liver mass. In the encysted stage the excretory granules seem to collect in the excretory bladder and present a dark Y-shaped mass, occupying the position of the muscular bladder. I have also observed encystment under the microscope. The cercaria slows down in activity, decaudation taking place by the action of the acicular spines of the lappets. The cercaria gradually contracts, and as the cyst wall appears, it moves round and round adding additional layers to the cyst wall. The suckers approach each other, and the excretory granules collect in the excretory bladder.

Discussion

Before dealing with the classification and systematic position of these two forms, I desire to direct attention to the differences between the two forms, which are as follows:

(1) The dimensions and the degree of activity.

(2) The absence of a conspicuous stylet in *C. gopyjungi*.

(3) The difference in the number of the salivary gland cells.

(4) The difference in the digestive system, viz. shorter caeca and oesophagus in *C. lühei*.

(5) The more posterior position of the acetabulum in *C. gopyjungi*.

(6) The size of the excretory bladder and the disposition and number of the flame cells.

(7) The difference in the size of the sporocysts and the degree of infection of the hosts.

These differences clearly show that these two cercariae are specifically distinct. The present-day classifications of the heterogeneous group of the Xiphidiocercariae are based on Lühe's classification. Lühe (1909, pp. 189–200) recognized only four different groups, namely: (1) Cercariae microcotyle, (2) Cercariae virgulae, (3) Cercariae ornatae, (4) Cercariae armatae. Cort created a subgroup of the group Cercariae armatae—the Polyadena group. The two cercariae described by me resemble this subgroup in the following features:

(1) Development in gastropods in sac-like or cylindrical sporocysts.

(2) Tail slender and less than the body length in the resting position.

(3) Acetabulum behind the middle of the body and approximately of the same size as the oral sucker. Caudal pockets with spines present.

(4) Stylet about six times as long as broad and with a thickening one-third from its anterior end. (Seen in *C. lühei* only.)

(5) Salivary gland cells lie between the acetabulum and the pharynx.

(6) A Y-shaped excretory bladder formed by the dilated portions of the main excretory ducts.

(7) A prepharynx and pharynx present followed by an oesophagus and intestinal caeca.

Later, Sewell (1922, p. 234) created another subgroup, the "Daswan group", based chiefly on the shape of the stylet and the length of the intestinal caeca. The absence in *C. gopyjungi* of the stylet thickening and the presence of a salivary gland composed of only three cells are characters of the "Daswan group", while the presence of an intestinal caeca reaching the posterior margin of the acetabulum is a character of the "Polyadena group". Hence *C. gopyjungi* bridges the two subgroups so far as the nature of the caecae is concerned. I therefore feel there is no necessity for these two subdivisions of the group Cercariae armatae, thus agreeing with Miller (1936) and Wesenberg-Lund (1931). We may, therefore, group together the characters of the Polyadena subgroup of Cort and the Daswan subgroup of Sewell and redefine the Cercariae armatae group of Lühe as follows from a study of these two forms:

(1) Developing in gastropods in elongate sac-like or cylindrical sporocysts.

(2) Tail slender and less than the body length, except when very much extended.

(3) Acetabulum behind the middle of the body and of approximately the same size as the oral sucker. Caudal pockets, armed with needle-like spines,

present (Indian forms) or no caudal pockets nor their spines present (European forms).

(4) Stylet with a thickening or with no thickening (viz. Daswan group of Sewell).

(5) Salivary gland cells three or more pairs.

(6) Excretory bladder and dilated portions of the main excretory tube divide into anterior and posterior collecting tubes. Total flame cells number either 12, 18, 24, or 36.

(7) A prepharynx and pharynx present followed by oesophagus and intestinal caeca which may be short or long.

TWO NEW SPECIES OF FURCOCERCOUS CERCARIAE

The infected snails were separated by placing them in groups of three or four in glass pots for about half an hour in the sun. The cercariae then come out and swarm in the water. The percentage of infection, however, is very low, being only about 2–3 % in *C. ajmeri* and about 1–2 % in *C. anasagari*.

The snails were collected from the Anasagar Tank, Ajmer. This tank is frequently visited by aquatic birds. The work was done during the rains and winter of 1936. Infection of the snails was highest in August and September.

Cercaria ajmeri n.sp. (Figs. 6–8).

This cercaria is larger than *C. indica* XLVII Sewell. It swims with an intermittent motion, usually with the tail end first and seldom with the head first. Cort has found this the method of locomotion in the cercaria of *Schistosoma japonicum* and, as Sewell (1922, p. 247) has pointed out, "though possibly not universal, it is at any rate of extremely common occurrence in all the furcocercous cercariae". It is never seen at rest with the head end upwards. It lies either parallel to the water level or with the head downwards and the furcae in a curve at right angles to the main stem. Under the binocular microscope its activity resembles that of a mosquito larva.

On the slide the cercaria performs characteristic wriggling motions and survives for a considerable time. It is capable of contracting and expanding considerably. It can be kept overnight in a glass pot.

The average measurements of the resting stage are as follows in mm.: length of body 0·288; its breadth 0·126; tail stem 0·666; breadth of tail stem 0·063; length of furca 0·234; its breadth 0·027; length of penetrating organ 0·102; its breadth 0·061; diameter of acetabulum 0·040; diameter of eye-spot 0·018; length of sporocyst 0·648; its breadth 0·324; length of caeca 0·044; its breadth 0·007.

The above measurements show that the cercaria is roughly twice as long as it is broad. The tail stem is about two and a half times the length of the body, while the furca is less than half the length of the main stem. The anterior end of the body is covered with pointed, piercing spines. The penetrating organ

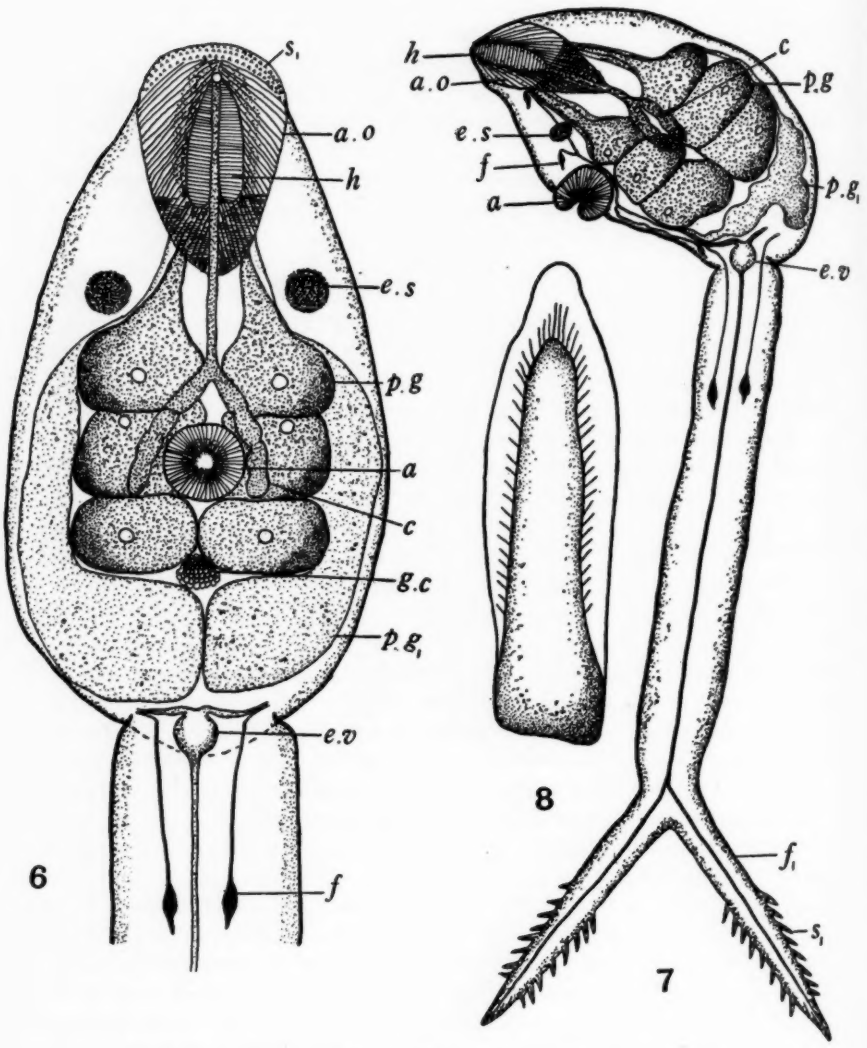

Fig. 6. *C. ajmeri.* Ventral view, to show the general anatomy. ×200.
Fig. 7. *C. ajmeri.* To show the excretory system. ×90.
Fig. 8. *C. ajmeri.* To show shape of furca immediately after death. ×200.

is a protrusible pyriform structure, extending up to about one-third the body length. Its posterior wall is muscular. There is a prominent head gland. The conical hollow spines which are said usually to cap the ducts of the penetration glands were not seen; probably they are masked by the anterior spines. The acetabulum is small and situated a little behind the middle of the body. Its wall is muscular and its opening is circular and armed with powerful spines. The tail is firmly attached to the body. Decaudation does not take place easily. The attachment of the tail stem to the body is peculiar. It is attached ventrally and firmly, a little anterior to the posterior end, a feature of not very common occurrence. The furcae are thickest at the point of attachment. Another peculiarity of this cercaria is that spines are not present on the furcae but needle-like processes are present on the body part of it. Similar needle-like processes lodged on the body of the furcae are shown by Rothschild (1938) in the fin-fold of Parapleurolophocerca cercaria. Furthermore, the cuticle of the furcae is in close contact with the needle-like processes; but, when the cercaria has stayed for a sufficient time on the slide, its activity slows down, and it is then seen that this cuticle becomes fluted and surrounds the furcae, giving the appearance of a diphycercal tail fin of a fish with the needle-like processes looking like the ribs. This probably is a consequence of the disintegration of the furca which starts first, assisted by the force exerted by the processes on the loose cells. The processes at the tip of the furcae are longest, being about 0·048 mm. in length. From here they diminish gradually along both sides. This cercaria might mistakenly be thought not to possess a fin-fold, for in the active condition the fin-fold lies in contact with the tail as in Fig. 7.

A pair of prominent eye-spots are situated about one-third from the anterior end. They are lateral in position, with a circular outline and a diameter of 0·018 mm., and are composed of a number of dark brown granules.

The mouth is small, situated on the ventral surface of the anterior organ. The ducts of the salivary glands enter on the ventro-lateral aspect of the anterior end of the organ. From the mouth passes an oesophagus, which traverses the anterior organ. At about the middle of the first pair of penetration glands it bifurcates into a pair of caecae. These reach as far as the posterior margin of the acetabulum. There are five pairs of penetration cells. Of these the anterior three pairs are coarsely granular and of a refractile nature. They are large cells with prominent nuclei and form a rectangular table enclosing the acetabulum in about the middle of it. The finely granular cells are in two pairs, lying laterally and one behind the other. Only careful observation of the active specimen serves to reveal the existence of two pairs, for very shortly after being on the slide the poorly defined margins merge into one another and thus give rise to the appearance of a mass occupying practically the whole of the posterior portion of the body. The nuclei of the finely granular cells are very indistinct.

In between the posterior penetration gland cells and the last pair of the anterior penetration gland cells, central in position, lie the germ cells in a mass.

As the cercaria does not give a good frontal view it is difficult to see the excretory system easily. The excretory system is of the true Schistosoma type. The excretory vesicle lies at the posterior end of the body. The main excretory tubes, arising from the antero-lateral margins, pass in a convoluted manner as far as the posterior margin of the acetabulum. There they divide into anterior and posterior collecting tubules. Each of the anterior collecting tubules divides into two capillaries, tipped with a flame cell. Each posterior collecting tubule passes backwards in a convoluted manner. It receives a capillary from a flame cell in its course, while the second capillary from the posterior collecting tubule enters the tail stem and passes backwards to end in a flame cell, lying in the caudal region. The caudal canal traverses the tail stem: it divides posteriorly and passes along the rami to open at the tips.

Both Miller (1926) and Sewell (1922) have made use of the number of flame cells of the excretory system in the classification of the Brevifurcate Distomes. More recently, Sewell (1930) has traced the probable lines of evolution of the excretory system in certain groups of the furcocercous cercariae. The Apharyngeal Brevifurcate Distome series includes two series of forms, namely, those that possess eye-spots (Schistosomatium series) and those in which these organs are absent (True Schistome series). In each of his evolutionary series (Test-fig. 1, p. 362) he commences with a simple system, such as is met with in the true Schistosomes, in which there are four pairs of flame cells, three pairs being in the body and the fourth in the tail stem, and of these two are connected with each collecting tube. In the Schistosomatium series, such a primitive condition, hitherto unknown, and doubtfully represented by *C. indica* XXXVI (Sewell, 1922, p. 263), is now definitely demonstrated by this form (*C. ajmeri*).

Development takes place in oval sac-like sporocysts with thin walls. They seem to contain the cercariae in the same phase of development. Sporocysts are 0·068 × 0·324 mm. An empty sporocyst leaves the collapsed wall dotted with the liver mass as long streaks. The sporocysts are brown in colour. I have also once seen a double infection of this form with an Amphistome cercaria of the Pigmentata group of Sewell.

Cercaria anasagari n.sp. (Fig. 9).

This cercaria was also obtained from the same tank as *C. ajmeri*, but it is much smaller in size. Infection of the snails was between 1 and 2 %. The cercaria is small and active and, like most furcocercariae, it swims with the tail end first with intermittent locomotion. The tail lashes the body while the furcae work like a pair of clippers. They prefer to float in water with the tail end upwards and the furcae in a curve at right angles to the tail stem. The fresh cercariae are greatly agitated by the slightest touch by any object and they dart to and fro in the water. On keeping they become quiescent but resume activity if disturbed. They also like to attach themselves by the penetrating organ and vibrate their whole body. On the slide they are at first very active and perform rapid wriggling motions. This soon slows down and

is followed by the leech-like creeping motion performed by the alternate use of the suckers. These cercariae are found by hundreds in a single snail. Decaudation on the slide takes place when death approaches. The following are the average measurements (in mm.) of the form when at rest: body 0·187 × 0·075; tail stem 0·245 × 0·037; furca 0·092 × 0·010; oral organ 0·065 × 0·037; acetabulum 0·020; sporocyst 0·051 × 0·034.

The body is capable of a considerable degree of contraction and expansion. The anterior penetrating organ is pyriform in shape, the posterior wall being muscular: it is protrusible and occupies slightly less than one-third of the body. A prominent head gland is present. The body is shorter than the tail stem. It is broadest just a little anterior to the acetabulum. The tail stem is attached terminally on the ventral side of the body, unlike *C. ajmeri*, in which it is attached more anteriorly; it is thickest a little behind its attachment to the body. The furcae are less than one-half the length of the tail stem. The acetabulum is a small protrusible muscular structure with a circular opening. It is situated about one-fifth from the posterior end. There are no eye-spots present in this form. The penetrating gland cells are in three pairs lying laterally. Two pairs lie in front of the acetabulum and the third behind it. Each penetrating gland cell is pyriform in shape with coarsely granular refractile protoplasm: their secretion is carried away by ducts which pierce the ventro-lateral aspect of the penetrating organ, and traverse its substance to open at the anterior tip.

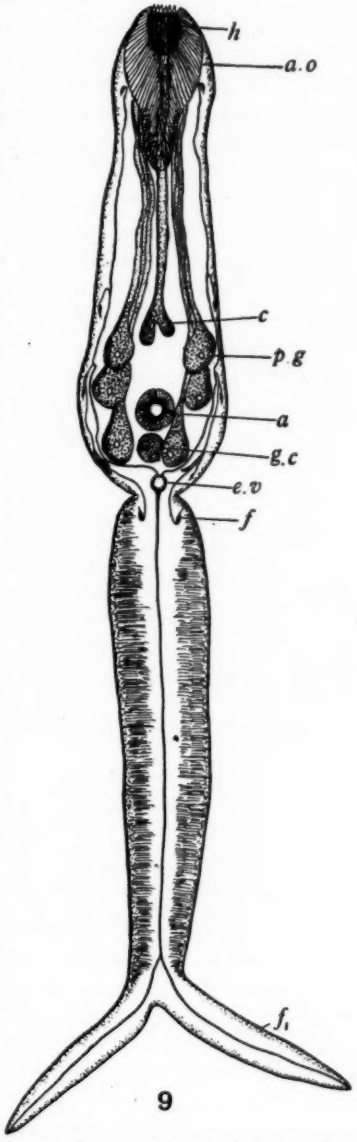

Fig. 9. *C. anasagi*. Ventral view to show the anatomy. × 170

The mouth appears to be situated anteriorly and ventrally. A thin oesophagus passes backwards through the substance of the anterior penetrating organ, and posteriorly divides into short, thick, globular caecae, measuring about

0·017 × 0·010 mm. in dimension. No spines were seen on the body, but the ducts of the penetration glands seemed to be capped with hollow cylindrical spines. The cercaria also gives a good frontal mount in most cases, for the acetabulum, although protrusible, is not frequently protruded by this form. Hence it simplifies the study of the excretory system.

The excretory system is simple. There are six pairs of flame cells. Two on each side empty into the anterior, and four into the posterior collecting tubule. Reference to Sewell's (1930) paper has already been made in the account of the excretory system of *C. ajmeri*. The type of excretory system as met with in *C. anasagari* is also of extreme importance from the evolutionary point of view as it also fills a gap in the true schistosome evolutionary series (Sewell, 1930, Text-fig. 1, p. 362). In the true schistosome series the simplest system of four pairs of flame cells is characteristic of the human-infesting schistosomes. From this stage the first step in the evolution of the series is represented by the "Spindale" group (Sewell, 1922). The next stage of evolution in his series, following the "Spindale" group, with a formula of

$$2 \times (1+2)+(3a+3b+4a+[4b]),$$

hitherto unknown, is now demonstrated by *C. anasagari*. Germ cells are seen lying ventral to the acetabulum.

The sporocysts are short, oval, sac-like structures lying in the liver mass. They are in contact with it and do not project freely. Their wall is thin and dirty brown in colour. They occur abundantly in the liver mass. I have once come across a double infection of the snail. The anterior liver mass was infected by this cercaria, while the posterior visceral loop was occupied by an Amphistome of the Pigmentata group of Sewell. The liver mass, due to the infection, assumes a bright brown colour and can be easily detected.

Discussion

The classification of the furcocercous cercariae has been a matter of considerable difficulty. Lühe (1909) included only the distomes in the furcocercous group and subdivided them on the basis of the presence or the absence of eye-spots. Cort (1917) divided the fork-tailed cercariae into three groups on the basis of the presence or absence of eye-spots and pharynx. With the subsequent descriptions of more forms, Sewell (1922), considering the presence or absence of an acetabulum to be of prime importance, separated out all the monostome forms. Faust (1932) laid importance on the excretory system as a basis for classification. Miller (1926) has divided the furcocercous cercariae on the basis of the presence or absence of a pharynx into two main groups—the Pharyngeal and the Apharyngeal, which probably constitute natural groups. The absence of a pharynx in *C. ajmeri* and *C. anasagari* places them in the Apharyngeal group. Furthermore, Miller (1926) has subdivided each of the main groups according to whether the individuals are monostomes or

distomes and brevifurcates or longifurcates and has defined the Brevifurcate Cercariae.

The following identical features place *C. ajmeri* and *C. anasagari* in the Apharyngeal Brevifurcate Distome series:

Furcae less than one-half the length of the tail stem. Body hyaline. Anterior organ a highly modified oral sucker. Ventral sucker much smaller than the oral sucker, very protrusible and often held protruded. Excretory openings at tips of furcae. Only a single pair of flame cells present in the tail stem. Caudal glands and sensory hair absent.

Finally, Miller has further subdivided the Apharyngeal Brevifurcate Distome Cercariae into eight subgroups designated A to H.

Group A, Miller (or Sewell's Group 1) is characterized by three pairs of flame cells in the body and one pair in the tail stem. As *C. ajmeri* has the above pattern it should be listed in this group.

Group C (or douthitti of Sewell, in part) is characterized by five pairs of flame cells in the body and one pair in the tail stem.

As *C. anasagari* has the above pattern it should be listed in this group.

SUMMARY

1. Two new species of Xiphidiocercariae have been described. These two forms have been designated as *C. lühei* and *C. gopyjungi*.

2. The flame-cell formula of *C. lühei*is $2 \times 3 \times 3 = 18$ and that of *C. gopyjungi* is $2 \times 4 \times 3 = 24$.

3. It is shown that *C. gopyjungi* has the characters of both the subgroups Polyadena (Cort) and Daswan (Sewell), and the group Cercariae armatae is redefined.

4. Further, two new species of furcocercous cercariae have been described. They have been designated as *C. ajmeri* and *C. anasagari*.

5. It has been pointed out that the types of excretory systems as met with in *C. ajmeri* and *C. anasagari* are of extreme importance from the evolutionary point of view and fill in gaps in Sewell's (1930) evolutionary scheme.

6. The latter two species have been listed in their proper position in Miller's (1926) scheme of classification of the furcocercous cercariae.

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EXPLANATION OF ABBREVIATIONS

a. acetabulum	*h.* head gland
a.o. anterior penetrating organ	*o.* oesophagus
c. caeca	*o.s.* oral sucker
c_1. cercaria	*p.* pharynx
c.c. cystogenous cell	*p.g.* anterior penetration gland cell
e.p. excretory pore	$p.g_1$. posterior penetration gland cells
e.s. eye-spot	*p.p.* prepharynx
e.v. excretory vesicle	*s.g.* salivary gland cell
f. flame cell	*s.* stylet
f_1 furca	s_1. spine
g.c. germ cell	

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BIOLOGICAL CONTROL AND THE THEORIES OF THE INTERACTIONS OF POPULATIONS

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(With 1 Figure in the Text)

CONTENTS

		PAGE
I.	Introduction	299
II.	Historical survey	301
III.	General theories of natural control	327
IV.	The problem of random searching	342
	(i) The general question	342
	(ii) Studies of field collected material	347
	(*a*) Crustacea	348
	(*b*) Myriapoda	349
	(*c*) Insecta	350
	(iii) The significance of the facts	355
V.	The mathematical formulation of the interaction of populations	365
VI.	Conclusions	380
	References	382

I. INTRODUCTION

Many great men have said that no science is really worthy of the name until it has attained quantitative accuracy and can express its principles and laws in mathematical form.

Economic entomology is mainly concerned with numerical questions. The financial loss the farmer or forester sustains from the work of injurious insects depends on the amount of damage per unit of area or material, and this, in turn, on the density of the pest population. The remedial measures adopted are determined by damage and pest density, and are limited by the necessity of securing a reasonable profit from the sale of the crop. Mathematical methods of various kinds must, therefore, play an increasingly important part in economic entomology and will certainly come to be regarded in the very near future as part of the fundamental equipment of every economic entomologist.

But in considering the application of mathematical methods to entomology, it must be remembered that its outstanding successes have been obtained in departments of research that are very different: such as the department of physics, which deals with things that are relatively simple and invariable, studied under conditions that can be defined and determined with extraordinary accuracy. In work with living organisms, carried on under experimental conditions, mathematical methods have given very valuable results, which can sometimes be usefully related to conditions in the field. Within certain limits they are applicable also to natural situations, enabling us to

discover the quantitative laws implied in our numerical data and estimate the significance of the differences in our samples. The results we obtain may be subject to controversy; but we are, at one point at least, in actual contact with facts.

There is, however, another method of attacking numerical problems. This consists in abstracting from the situation as it exists in nature the quantitative elements and relations regarded as fundamental. These are embodied in a mathematical formulation, which can then be dealt with by purely deductive methods.

When we are studying the properties of things that are natural unities, there is little risk in this method. The mathematical hypothesis we make about the growth of a snail-shell or a horn, or the form of a liquid drop, though it may be in the first instance little more than a guess or intuition, gives deductions that can be immediately tested and verified.

But the situations with which the economic entomologist has to deal are not of this type. He is mainly concerned with the interaction of populations. The worker in the field of biological control, for example, is concerned, in the majority of his operations, with a population of parasitic or predaceous insects acting on a population of an insect or plant pest. The collection of data in the field is difficult and expensive. In many cases events develop with discouraging slowness, while the results are hard to interpret. Nevertheless, the actual situation seems fundamentally fairly simple and one easily formulated in mathematical terms.

There is thus, for workers in biological control and kindred subjects, a natural and almost irresistible impulse to biomathematical speculation. The present writer happens to have been one of the first to take up this work. He must, however, confess that it was some time before its exact significance and limitations became clear to him. In the meantime, largely owing to the energy and enthusiasm of the great Italian mathematician Vito Volterra, inspired by the biologist Umberto d'Ancona, the mathematical theory of populations had taken on a remarkably comprehensive and impressive character. Designed, by the present writer at all events, as a humble accessory to normal methods of investigation, it has gradually come to assume a dominant position. Volterra's views as to the significance of his results, though at first unexceptionable, seem to have become, with the passage of time, more positive and dogmatic. Finally, some workers in the field of biological control have apparently decided that the mathematical theories may be considered in some sense as a substitute for observation; that the study of them will reveal to us the facts of nature; and that we may be guided by them in practical work. Entomologists untrained in mathematics might find these conclusions rather discouraging since they would be obliged either to accept on trust principles they do not understand and cannot justify, or to undertake a lengthy course in difficult mathematics.

The present writer is convinced that this view is mistaken; that the mathematical theories, though a natural and useful development, have not

the significance attributed to them; that none of the theories so far produced can be considered as an adequate representation of events in nature, while the theory at present dominant, being of a form derived from physical phenomena, is particularly inapplicable to the behaviour and interaction of living organisms; and that observation and experiment are still the only safe basis for practical operations in economic biology.

The second part of this paper gives a brief historical review of the subject, the third deals with general theories of natural control, the fourth with the hypothesis that organisms search at random, fundamental to the dominant theory, while the fifth contains a summary of the principal mathematical formulations constructed up to the present time.[1]

II. HISTORICAL SURVEY

Population studies have, of late years, tended to assume a markedly mathematical character. Mathematics is simply the science of quantity. Any treatment of a problem that restricts itself to quantitative values is mathematical, whether it deals with definite specific numbers or with indefinite numbers designated by algebraical symbols. The simple arithmetical calculations made by some of the pioneer workers in biological control therefore constitute a mathematical theory of the subject just as truly as the complex and imposing edifices constructed with the tools of the infinitesimal calculus by the expert mathematician, and since they were produced by men in touch with the facts deserve just as careful study.

But a mathematical theory can only be constructed within a framework of qualitative postules. Certain facts of animal behaviour or assumptions concerning it constitute the framework of the mathematical theory of population problems. The fundamental facts in the theory of populations of living things are the three fundamental functions, nutrition, growth, and reproduction. As organisms feed and grow, and must draw their food supplies from outside themselves, they are continually diminishing the very thing they require for existence; as they not only reproduce, but also multiply, the diminution of the food supply becomes, generation by generation, more severe. Malthus, the founder of population studies, meditating on these facts, and making calculations on the assumption that while organisms increase in geometrical progression the food supply increases only in arithmetical progression, and considering that the reproductive instinct is as impossible to arrest as an avalanche, concluded that in nature the increase of organisms goes on until it is checked by famine, pestilence and war, engendered by their excessive numbers. This principle, taken over from Malthus by Darwin, became the basis of his theory of evolution. "Every single organic being around us", says Darwin, "may be said to be striving to the utmost to increase in numbers"... "heavy destruction inevitably falls either on the young or old, during each generation, or at

[1] The writer is indebted to Dr M. G. Walker and Mr H. S. Hanson for reading the manuscript of this paper and for many valuable suggestions and criticisms.

recurrent intervals. Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount."[1] The fact that the control of populations is sometimes biological control, did not escape Darwin. "The amount of food for each species", he says, "of course gives the extreme limit to which[2] each can increase; but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species"; and in another place he suggests that the increase of species is sometimes checked by epidemics of parasitic worms, which may have been disproportionately favoured "through facility of diffusion among the crowded animals".[3] It is clear that, on these principles, the multiplication of the worms would eventually cause a reduction in their food supply, and, consequently, a fall in their own numbers; so that we might expect to find oscillations in the populations of pest and parasite.

Forty years later, the fact that such oscillations do occur was independently noted by two entomologists, P. Marchal and L. O. Howard. "There are" wrote Marchal (1897), "certain insects whose numerical evolution could be represented by a curve with great oscillations, each of them characterized by a period of rather slow ascent and a sudden vertical descent." This curve, he says, is particularly evident in the case of certain insects injurious to agriculture, such as the Hessian fly, oat midge, army worms, etc., and is usually due to parasites. The parasitic species has a curve of numerical evolution which runs along that of the host during the ascending period; at a certain moment the curve of the parasite meets that of the host and the united curves then fall suddenly together. This, says Marchal, would indicate the extermination of the host followed by that of the parasite, were it not for the fact that the life history of the pest species is very variable. Owing to this fact, there are always reserves of the host species that escape the parasites and form the point of a new invasion.

In his paper on the parasites of the white-marked tussock moth, L. O. Howard (1897) reached practically the same conclusions. "Whenever a plant-feeding species, from some cause or other, transcends its normal abundance to any great extent, there is always", he says, "a great multiplication of its natural enemies, and this multiplication is so great as to reduce the species even below its normal." There are, he admits, "specially protected species" that have no natural enemies, but even here "disease steps in and fills the want", and he instances the Chinch bug as a case in point. "With all injurious lepidopterous larvae, however", he continues, "we constantly see a great fluctuation in numbers, their parasites rapidly increasing immediately after the increase of the host species, overtaking it numerically and reducing it to the bottom of another ascending period of development."

The outbreak of the white-marked tussock moth, studied by Howard, was a striking example of what he described. In the late summer of 1895, he says,

[1] *Origin*, ch. III, p. 63. [2] *Loc. cit.* p. 64. [3] *Loc. cit.* p. 66.

"almost every poplar, soft maple, box elder, elm, alder, birch and willow in the City of Washington was completely defoliated, while the maples, sycamores, horse-chestnuts, ashes, and many other trees were badly damaged. The rapidly developing parasites had, by this time, become so numerous that it was an exception to find a healthy caterpillar which one of the parasites was not engaged in stinging. The rearings which were undertaken at this time show a parasitism of perhaps 90% of the caterpillars.

"About 10% of the cocoons at the end of September gave forth adult moths, and of these, of course, only about half were females. Ten per cent then of the possible females of the fall generation laid their eggs, and the majority of these eggs hibernated successfully, so that in April and May 1896, there was a moderately abundant hatching of young *Orgyia* caterpillars.

"In the meantime, however, the extremely abundant primary parasites had successfully hibernated and were in a position to make their position felt. It resulted that, at the points of observation this first generation of tussock moth caterpillars was practically exterminated, and in June it was a very difficult matter to find enough living individuals to carry on rearing-cage experiments at the very points where they had been present the previous year by thousands and thousands." In the later months of the year, however, the presence of hyperparasites was noticed; and by the time the third generation of tussock moth caterpillars became full-grown, it was no longer so difficult to find specimens as it had been in June. Nevertheless, they were still rare and their partial recuperation must, says Howard, "be attributed almost entirely to the work of hyperparasites".

An explanation of the scarcity of parasites at certain points is also given by Howard. "The tussock-moth", he says "is a slow traveller. Its primary parasites naturally congregate at the point of greatest caterpillar abundance. At points where the caterpillars are scarce they are thus less exposed to the attacks of their parasitic enemies, and it results that there may actually be an increase of the species at one point simultaneously with a decrease at another."

In 1903, W. F. Fiske published the results of a study of the parasites of the American tent caterpillar carried on from 1896 to 1900 inclusive. He expected, he says, that the parasites "would be found to be one of the more important of the factors that governed the abundance of the species from year to year". He followed it from a season in which it was extremely common, to a year in which it was considerably below normal abundance, but he did not find evidence that the parasites had produced this fall in numbers. "The parasites as a body", he states, "were found to exact a certain tithe of blood, so to speak, and this being obtained would proceed to fight over its possession, passing it from one to another, from parasite to hyperparasite until often, perhaps, there would be little more than enough left of a single large caterpillar than that sufficient to support a single small Chalcid." The variations in the numbers of the tent caterpillar were, Fiske thought, due to causes other than

the parasites. The fluctuations in the numbers of the parasites themselves he believed to be due largely to the attacks of the hyperparasites. The fact that the primary parasites were not in fact able to reduce the numbers of the host to a minimum was, in his view, to be attributed partly to the influence of the hyperparasitic species and partly to the fact that the life history of some of the primaries does not synchronize with that of the host, so that they have to pass through several generations on other species, some of which may be scarce at the time the parasite requires them. "In the case of the hyperparasites they can follow their hosts throughout the season, suffering when they suffer, but preying on them in their prosperity."

In 1907 Marchal published a general paper on the utilization of entomophagous insects in the struggle against insects injurious to agriculture. In the first section of this paper he discusses the general problem of the natural control of phytophagous insects and the part entomophagous insects play in it. His remarks, though brief, are remarkably clear and comprehensive and constitute an important advance in the general treatment of the subject. He considers that the limitation of the damage done by phytophagous insects is largely due to their parasitic and predaceous enemies. He notes that some, like the egg parasites, kill the host before it can do any damage, while others do not destroy it until it has finished feeding and thus act merely by lowering the reproductive rate of the pest.

"When, on account of cultural conditions or climatic circumstances or other influences, the phytophagous species tends to increase beyond the average", says Marchal, "it thus furnishes conditions eminently suitable to the multiplication of the parasitic species, and that in its turn causes the phytophagous form to decrease."

In this paper we see, for the first time, so far as the present writer is aware, the outline of a mathematical theory of biological control, extracted by Marchal from a little known work by two French authors, Bellevoye & Laurent (1897). A case is studied arithmetically, the assumptions being that the population of the pest considered is four times that of the parasite population, that host and parasite each lay 100 eggs, that in both species the number of males and females is equal and that the parasite places one egg in each caterpillar attacked. On this basis it is shown that in four generations the pest will be annihilated by the parasite. Marchal asserts that incidents like this are frequently observed in nature and that "it is almost always to the work of parasites that the rapid retrocessions of injurious species must be attributed", and he cites examples in support of his belief.

Marchal points out, however, that such violent oscillations of pest and parasite are not the invariable rule. "In other cases which more nearly approach the general and primitive law of nature", he says, "the injurious species maintains always about the same rank, and the fluctuations which it presents are only of secondary importance. The parasites act as a moderating check to the continued increase and prevent the injurious species from multi-

plying in an excessive manner. They are themselves present in almost constant numbers from year to year. Their role is not only to bring back an injurious species to a small number of individuals when it has passed the mean, but to hold it constantly at a numerical point much below that which it would reach without their presence." To show how such a condition can exist, Marchal reproduces, from Bellevoye & Laurent, the algebraical equation

$$\frac{c}{b}=\frac{a-1}{a},$$

in which c represents the number of eggs laid by an individual of the parasitic species, b the number of eggs laid by an individual of the plant-feeding species, and $(a-1)/a$ the proportion of parasitized insects. Here we have the first algebraical formulation of this problem and, what later authors have called, the equation of the "steady state", in terms of the initial assumptions utilized.

Marchal takes care to point out that the two types of host or parasite interactions are more theoretical than real, and that all possible intermediate stages between them exist in nature. Control cannot, he says, be attributed to any one parasitic species but is dependent on many factors, some of the most important of which are (1) the hyperparasites, (2) the co-parasites, (3) other plant-feeding species occurring with the host species, (4) the enemies of insects in general (insectivorous birds, etc.), (5) climatic conditions, (6) the rapidity of multiplication of pests and their enemies, (7) the tendency in the plant-feeding species to retard the development of certain individuals of a given generation for a longer or shorter time, (8) a similar developmental variability in the parasitic species.

Thus *Encyrtus*, which is an important enemy of *Hyponomeuta*, has an oviposition period notably shorter than that of its host; the hymenopterous parasites of the Hessian fly have only two generations a year, and the duration of these is relatively constant, while the pest has five or six generations, whose duration is very variable.

In 1907, W. F. Fiske was placed in charge of the American work on the parasites of the gipsy and browntail moths, carried on under the immediate supervision of L. O. Howard. Both of these entomologists were peculiarly fitted by training and inclination for the investigation, and, as a result, a great many important advances were made in the practical and theoretical study of natural control and the parasite-host problem. The most important of these are to be found in the well-known *Technical Bulletin* no. 91 by Howard & Fiske, published in 1911 by the United States Department of Agriculture, and a paper by Fiske on the phenomenon of superparasitism, published in the *Journal of Economic Entomology* in 1910.

Howard & Fiske state that the potential rate of increase of the gipsy moth, judged by the average number of eggs deposited, is 250-fold per annum. The average annual rate of increase had been estimated by Forbush & Fernald to

be actually about sixfold. Howard & Fiske show that the complete prevention of increase would require a real mortality of 99·6% per annum, and they point out that if we begin with the larvae hatching from a mass of 500 eggs, this means an apparent mortality of 50% during each of the seven larval stages and a mortality of 25% during the prepupal stage. If the actual increase is sixfold and we wish to ensure absolute stability, it will be necessary to have a further destruction of 83·33% of the surviving progeny of the gipsy moth. Owing to the form of the egg masses, a large proportion of eggs is inaccessible to the only egg parasites known to exist. A succession of parasites attacking subsequent stages will therefore be required. It is, of course, conceivable that *one* further parasite might be sufficient, but since Howard & Fiske found that a sequence attacking larval and pupal stages really is associated with control in the native home of the gipsy moth, they considered that it would probably be necessary to introduce such a sequence into America.

Consideration of the way in which control might be effected, led Howard & Fiske to distinguish between the various groups of factors involved in such a process. In a country in which conditions are settled, they say, an insect "neither increases to such an abundance as to be affected by disease or checked from further multiplication through lack of food, nor does it become extinct, but throughout maintains a degree of abundance in relation to other species existing in the vicinity, which, when averaged for a long series of years, is constant". For this, "it is necessary that among the factors which work together in restricting the multiplication of the species, there shall be at least one, if not more, which is what is here termed facultative (for want of a better name) and which, by exerting a restraining influence which is relatively more effective when conditions favour undue increase, serves to prevent it". Climatic agencies, such as drought, frost and storm, may, on the other hand, be classed as "catastrophic" factors; the average percentage of destruction they effect "remains the same, no matter how abundant or how near to extinction the insect may have become". Finally, such predators as birds work in a radically different manner. They "are not directly affected by the abundance or scarcity of any items in their varied menu". The destruction they effect is therefore constant from year to year, or, "if variable, is not correlated in its variations to the fluctuations of the insect preyed upon"; and "would most probably represent a heavier percentage when that insect was scarce than when it was common".

"In effect", conclude these authors, "the proposition is here submitted as a basis for further discussion, that only through parasites and predators, the numerical increase of which is directly affected by the numerical increase of the host insect on which they prey, is that insect to be brought under complete natural control, except in the relatively rare instances in which destruction through disease is not dependent on superabundance."

Remarks made by certain later authors suggest a belief that Howard & Fiske, in stating that the numerical increase of the parasites is directly

affected by that of the host, refer to the influence of host density on the reproductive rate of the individual parasite. But as we have seen, Howard, in his bulletin on the white-marked tussock moth, refers to the tendency of the parasites to congregate at points where the host is abundant, so it seems possible that this is the way in which Howard & Fiske in their joint (1911) paper, envisaged the effect of increase in host density. Furthermore, the simple fact that a parasite population increases at the expense of the host population, whether the individual reproductive rate varies as a function of host density or not, entitles parasites to be classed as "facultative agencies", as opposed to climatic factors, when climate acts in the way described by Howard & Fiske.

In his paper on superparasitism, Fiske studied the question of the distribution of progeny by parasites. It had generally been supposed that the parasite selects its hosts in the best interests of its offspring, depositing its eggs only in individuals that are unparasitized, or will support several parasite larvae. The observations made at the Gipsy Moth Laboratory showed the parasite females often confide their offspring to hosts already parasitized, by the same or another species, and that in these cases some or all of the parasites may die without completing their development. This fact led Fiske to the idea that parasites distribute their progeny among the available hosts at random. On the basis of calculations he made, he gave a curve showing the probable percentage of parasitism resulting from the distribution of 1, 2, 3, ..., etc., eggs at random among 100 individuals of the host. He considered that the losses due to the random distribution of progeny might greatly reduce a parasite's chances of exerting effective control of an insect as fecund as the gipsy moth, and he found in the rapid increase in mortality from this cause, as the ratio of eggs deposited to hosts present rises, an additional argument for his belief that a sequence of parasites is required for control.

The admirable work carried out by entomologists working in Hawaii, though most successful from a practical standpoint, did not produce many published contributions to the theory of biological control, though I was told by the late Dr Frederick Muir that the question of the suitability of parasites for the control of particular pests received great attention; and he attributed the success attained mainly to this fact. He himself, in his Presidential Address to the Entomological Society of Hawaii in 1913, discussed arithmetically a number of cases of parasite-host interrelations. He described the conditions for stability of population, showed how, owing to a higher rate of survival, an introduced species could rapidly replace an endemic form limited to the same area of distribution, how differential susceptibility to natural enemies might quickly produce very great changes in the relative value of the populations of several species, and how a host may continue to increase even when the parasite is destined to exterminate it within a few generations.

Several other important remarks were made by Muir in this paper. He says that "among phytophagous insects, there is never a direct struggle, and

only on rare occasions, and as an abnormal phenomenon, is there a shortage of food which causes direct competition". After mentioning the fact that there is often, over wide areas, a constant ratio between the numbers of a host and its parasite, he suggests that this ratio depends "on the capacity of the parasite to discover its host"; and that the decrease of the host produced by the parasite must ordinarily arrest the increase or destructive power of the latter before extermination can take place. A more efficient species controls the host at a lower population level than one whose searching capacity is less. Predators, he considered, are a more mobile death-factor than parasites.

In 1922, J. D. Tothill, who had formerly been associated with W. F. Fiske, H. S. Smith, C. W. Collins, and the present writer in the Gipsy Moth Parasite Laboratory in Massachusetts, published an important paper on the natural control of the fall webworm (*Hyphantria cunea* Drury), containing the results of studies made in Canada, in collaboration with A. B. Baird & Alan Dunstan. He made an effort to evaluate exactly, over a series of years, the part played by the various biological factors—including infertility and the insectivorous birds—in the control of the webworm. He found that, in 1912, when the host was abundant, it was attacked by eight species of parasites which were responsible for a total mortality of 78%. Following this the webworm became uncommon and declined steadily in numbers until 1916, when it was almost extinct. Concurrently, the parasites decreased in numbers and destructiveness, so that in 1916 none at all were found in the collection. In 1917 parasitism rose to 15%, while in 1918 it was about 13%. In these two years the population rose slightly. The proportion of caterpillars destroyed by birds was, roughly speaking, inversely proportional to the density of the webworm population, being about 11·5% in the year of greatest abundance, and about 90% in the year of greatest scarcity. Tothill believed that previous to 1912 the webworm population had been relatively stable for a considerable period, with the parasitic enemies gradually gaining ground. In 1912 the parasites reached, in the Province of New Brunswick, a level where they caused an abrupt fall in the numbers of the host, which continued thenceforth to decline. "During this period", says the author, "the parasites became exposed to conditions they were unable to meet and one by one they dropped out of the contest." What saved this moth from extinction was not, however, the inherent power of recovery of the specimens still present, but a sudden influx of moths across the Bay of Fundy from the Province of Nova Scotia. This sudden migration of insects unaccompanied by their natural enemies into a region where the latter had become almost extinct through lack of hosts, enabled the webworm to regain its place in the local fauna. Following this, a gradual recovery of the parasites was noted, though the diminution in the numbers of the webworm in 1913, 1914 and 1915 caused the elimination from the Province of New Brunswick of the major parasite, *Campoplex validus* Cress., through starvation. The outbreaks studied by Tothill were, according to him, facilitated by the abundant food supply provided by the addition of large areas of a new food

plant—the apple—to the scattered clumps of swamp alder (*Alnus incana*), which was the original plant host; and their immediate cause was, in every case, the temporary scarcity of parasites combined with a sudden influx of moths from other areas.

It is clear, from what has been said, that Tothill and his collaborators carried out their investigations with an eye to the fundamental problems involved, so that their results have an important bearing in theory, though this is not explicitly treated.

On the other hand, the data are not presented in a way sufficient to establish some of the author's theses. In the table (p. 15) summarizing the results of the work at Frederickton, N.B., the reproductive rate of the moth is assumed to be invariable at 260, throughout a 7-year period. In each year one individual is said to survive from the egg mass; yet the population is falling during a great deal of the period referred to. The number of individuals destroyed by birds is in each year exactly what is required to make up the total of 260 offspring that have to be accounted for in each generation, though destruction by birds is notoriously difficult to estimate. All Tothill's tables are constructed on the same model, and all give the impression that the data have been over-simplified in preparing them for publication. Nevertheless, the paper is interesting and suggestive and deserves careful study.

The work of the French naturalist, E. Rabaud, though not specifically in the field of biological control or animal populations, deserves mention here because of his comprehensive "Essai sur la vie et la mort des espèces" published in 1917. This paper is really directed against the Darwinian idea that a struggle for existence resulting in the survival of the fittest, exists in nature; but it contains a remarkably interesting survey of the general problems with which we are dealing. Rabaud considers that the interactions of organisms are dominated by the phenomenon of specific affinity working either through active attraction or through passive displacement. He points out the importance of the factors of density and quantity, and shows how specific attraction and the chance of encounters are affected by their values. The existence of factors whose intensity increases with the multiplication of individuals in the assemblage on which they act, is clearly recognized by Rabaud. But though the oscillations of populations observed when such factors are involved give one the impression of an equilibrium, this idea, he says, is really unjustified. The rise and fall in the numbers of organisms and their eventful fate depends on the action of a multitude of interacting factors —climatic, edaphic, organic—which are constantly changing in direction, intensity, and species. The notion that the observed effects can be ascribed to any definite controlling mechanism is therefore an illusion, nor can we say, at any given moment, that an equilibrium exists in the sense that the places left vacant by deaths must automatically be filled up as they become empty. Many suggestive and interesting facts are brought forward in this work by Rabaud, though it has attracted little attention.

The present writer began work on the problems of biological control in the Gipsy Moth Parasite Laboratory, in Massachusetts, in 1908, under the direction of W. F. Fiske and C. H. T. Townsend, in association with H. S. Smith, J. D. Tothill, C. W. Collins and other entomologists, many of whom have made important theoretical and practical contributions to the work. In 1912–13, he carried out, at first in collaboration with W. F. Fiske, H. S. Smith and the late L. H. Worthley, an investigation of the parasites of the gipsy moth and the alfalfa weevil (*Hypera variabilis* Hbst.) in southern and western Europe. During the War, the study of D'Arcy Thompson's admirable book, *Growth and Form*, stimulated his interest in the mathematical aspect of biological questions. In 1919, while working in the University of Paris, he was asked by Dr L. O. Howard to undertake the study and collection of the parasites of the European corn-borer (*Pyrausta nubilalis* Hb.), recently imported into the eastern United States. He was thus led, in 1920, while working in south-western France, to develop a simple algebraical formulation of the quantitative relations between a pest and the parasite reproducing at its expense. It was found that if we represent by algebraical symbols the number of hosts, the number of parasites, their particular reproductive rates and their sex ratios, we can, on the basis of certain simple assumptions, produce equations giving the number of hosts and parasites in the tth generation. A paper embodying these formulae was submitted in 1921 to the officer in charge of the corn-borer investigation; but he considered the treatment too difficult from the mathematical standpoint to be of use to entomologists. Prof. Paul Marchal was, however, interested, and in 1922 he presented to the Academy of Sciences in Paris four notes prepared by the writer. In the first, entitled "Théorie de l'action des parasites entomophages; Les Formules mathématiques du parasitisme cyclique", the writer drew attention to the evidence for the existence of rhythmical or cyclical variations in the numbers of injurious insects, referred to the statement of L. O. Howard in his bulletin on the white-marked tussock moth, where the phenomenon is attributed to the action of insect parasites, and suggested that the cyclical or periodic character of the natural process indicated the possibility of a mathematical representation of it. He was careful to point out that for the study of the parasitic cycle exact observations of the phenomena in the field were a prime necessity; but he affirmed that for a scientific treatment of the problem a mathematical representation was also required—an assertion based on the fact that the relations to be studied were numerical and quantitative in character. The formulae were deliberately constructed so as to include only the factors believed to be fundamental, i.e. those which must be included in *all* representations of the problem. For that reason, he said at the end of the note: "Ces formules fondamentales constituent la base de l'étude théorique de l'action des parasites entomophages." The next note, which followed a little later, carried the subject a little further and gave, after some simple transformations, the formulae for the duration of the parasitic cycle and the proportion of hosts parasitized when the reproductive rates of the parasite is

equal to, less than, or greater than that of the host, a new symbol being introduced to express the ratio between reproductive rates. The two remaining notes, in the *Comptes Rendus*, referred to the necessity of introducing factors, not yet considered, into the mathematical representation. A number of specific numerical examples were given, illustrating the character of the parasitic cycle, comparing the values obtained when a parasite reproduces at the host's expense to those found when the latter reproduces unchecked, and showing how variations of the values of the various factors involved, affects the numerical sequences derived from the formulae. Attention was drawn to the significance of those results in regard to practical operations. In 1923 a more comprehensive paper on the subject was published at the suggestion of Prof. Marchal, in the *Revue Générale des Sciences*. In this work the writer clearly indicated his belief that though some of the curves derived from theory imply the annihilation of the host, this does not ordinarily occur in fact. The host continues to exist at a lower level, and in such cases a temporary increase in its numbers will probably be followed by a rise in the parasite population (*loc. cit.* p. 6, col. 1, footnote 1, col. 2). The importance of considering dispersal rate in the case of introduced parasites is also treated. In the same paper the writer dealt with the problem of the combined action of several parasites, with different rates of reproduction; with social parasitism (where several offspring of the parasite develop in a single host); with asynchronous parasitism (where there is discordance between the life cycles of host and parasite); and with the action of hyperparasites, giving, in the latter case, the general formulae for (1) a parallel and indefinite increase of host, primary parasite and hyperparasite, without "extermination", or (2) a continuous fall in the host population. A formula showing the conditions in which host and parasite populations remain constant from generation to generation, so that we have what the physicists and some of their entomological followers call "the steady state", was given, and it was shown that this can be obtained by postulating the inaccessibility of part of the host population to parasite attack. The belief, expressed by E. Picard, that the development of a parasitic cycle partly depends on the existence of a close specific relation between host and parasite was also mentioned. The contribution of Bellevoye & Laurent, to which the writer's attention had been called by Prof. Paul Marchal, was recognized. The limits of the mathematical method were clearly defined. "Ces formules", said the writer, "représentent à notre sens ce qu'il y a de fondamental dans le rapport entre parasite et hôte. Les conclusions que nous pouvons en tirer doivent donc avoir aussi une valeur générale. Non pas que ces conclusions seront toujours rigoureusement d'accord avec les faits. Tant s'en faut. Mais on peut du moins les considérer comme un thème sur lequel la nature brode les infinies variations de la réalité et à ce titre elles constituent une base théorique pour notre travail."

In the following year the methods developed were utilized in a discussion of Fiske's *Sequence Theory* of parasite control. On assumptions originally

adopted, the effect of accumulating parasites with different reproductive rates was examined, the general conditions necessary for the establishment of a "permanent equilibrium" between host and parasite, when several species of parasites act together, were broadly defined, and it was shown that under certain conditions of spatial and temporal distribution this could in fact be realized in nature. The idea that parasites acting in a sequence should necessarily be introduced against an imported pest was therefore rejected: (1) as a valid general theory, because "it applies simply to a very limited group of special cases", defined as "blocked cyclical parasitism", which are "much less important for the theoretical study of parasite action than pure or uninterrupted cyclical parasitism", of which, it was said, "they are simply derivatives"; (2) as a practical policy, because it is often impossible of realization and because the real desideratum is not merely the reduction of host numbers to a stable condition, at which Fiske's theory seemed to aim, but the practical extermination of it. The necessity of introducing parasites "fitted to all of the various environments in which a host is found" was also referred to.

From the earliest stages of the theoretical work an effort was made to incorporate the idea of random distribution in the mathematical formulae. It was, of course, easy to utilize Fiske's well-known curve for arithmetical calculations; but a general solution of the problem was desired. The present writer succeeded in solving the distribution problem, using the calculus of probabilities, but this did not give a workable solution. This was eventually obtained (in 1920) through the help of Prof. Deltheil, the well-known authority on probability problems. Some simple modifications, suggested by Prof. Péres of Marseilles, enabled the writer to incorporate the theory of random distribution in his general formulation and give a general mathematical solution of the problem of the parasitic cycle as modified by the factor of chance distribution, as well as a table of values useful in further work and some definite examples. This paper was first sent to Cambridge, but no avenue of publication was found for it and it was returned with adverse criticism from a referee, based not on mathematical but on entomological grounds. It was therefore rewritten in French and published, through the help of Prof. Péres, in the *Annales de la Faculté des Sciences de Marseilles.*

In 1927 the writer returned to the mathematical theory with a paper designed to show how, using the assumptions made, the progress of introduced parasites might be calculated and the validity of the assumptions themselves tested, by comparison with events in the field. Later in the same year, the fundamental equations were recast so that they could be applied to the problem of the effect of methods of mechanical control on the progress of introduced parasites of insect pests. In 1928 the relative value of parasites and predators was studied from the biologico-mathematical standpoint. In this paper the fact that species with high *potential* reproductive rates do not necessarily have a greater *effective* rate of reproduction than those with low potential reproductive rates was definitely stated. The idea involved in the

theory of cycles, that the scarcity of hosts limits the effective reproductive rate of the parasite, while an abundance of hosts causes it to rise, is also stressed. In 1929 the problem of the parasitic cycle, in cases where a fixed proportion of the host population is inaccessible to the natural enemies, was dealt with. The conditions producing stability of population were also discussed. In this year the assumptions regarding random distribution were modified. In the 1924 paper it was assumed that *all* eggs deposited in hosts gave rise to adult parasites, no matter how numerous they are; in the 1929 paper other possibilities were discussed, and the one examined was that *one* parasite emerges from each host attacked. The results of this modification were shown by a study of equations and by numerical examples. In 1930 a short paper covering the general questions of mathematical methods, their significance and utility, was published in the *Annals of Applied Biology*; and various ways in which the fundamental formulae could be modified were mentioned, including one, suggested to the writer by Prof. Cook of Montana in 1928, allowing for modification of the reproductive rate of the parasite in relation to variations in host density. The studies of the parasite-host interaction as a continuous function, made by Lotka and Volterra, were also mentioned and the advantages of the discontinuous functions indicated. Another suggestion regarding the factor of density was made by the writer in a comprehensive study of the method of biological control published by the Empire Marketing Board in 1930, and will be utilized later in the present paper. Finally, in 1931, a mathematical treatment of the problem of the reproduction of organisms with overlapping generations, on which the writer had been working for many years and had completed with the help of the late H. E. Soper, was brought out.

From the earliest stages of this investigation, the writer tried to define as accurately as possible the scope and significance of mathematical theory as applied to biological questions. A paper dealing with the significance of the physico-mathematical method in morphological problems was published in 1929. In 1930, in the Empire Marketing Board *Bulletin* already referred to, some of the peculiar dangers of this type of work were pointed out. In 1937, in a book, *Science and Common Sense*, on the general theory of science, an attempt was made to deal with the fundamental principles involved (*loc. cit.* chap. VI, "The Use and Abuse of Mathematics"); and to this, an essay in *Science Progress* (October 1938) on Dr Woodger's *Axiomatic Method in Biology* adds some complementary material.

Work on the general theory of natural control was carried on at the same time, in collaboration with Dr H. L. Parker in connexion with the corn-borer investigation and other practical projects, in southern France, and continued later at Farnham House Laboratory. Since it was clear that the problem of host selection by parasites—which is, of course, merely an aspect of the general problem of food selection by organisms—is of fundamental importance, an attempt was made, after an experimental study of the parasite *Melittobia*

acasta Walk., to get to the bottom of the subject, and the results were published in 1927, in this journal. In 1928 the writer discussed the question of biological control in continental areas, taking up the problem of factors acting in a sequence, pointing out the fact, made clearly evident by the corn-borer studies, that the complex of factors involved in the natural control of an organism differ in different times and places. The explanation suggested for this fact was felt at the time to be inadequate. In 1929, therefore, the writer returned to the subject and in a short paper, "On natural control", briefly sketched what he believed and still ventures to consider to be the basic explanation of the phenomenon of natural control.

In the meantime, of course, many other workers had been investigating the same problems. In 1922, F. Picard published a paper on the parasites of *Pieris brassicae* L. He noted the fact that the parasite complex attacking *Pieris* is different in each region and, nevertheless, manages to maintain some kind of equilibrium; and he stressed the necessity of studying the assemblages that actually exist in nature. The constant high parasitism of *Pieris* is due, he thought, to the following facts: the parasites attacking it are all more or less polyphagous, as much, or more strongly attracted by *Pieris* as by their other hosts, but able to subsist without it, when it becomes uncommon; the generations of *Pieris* overlap in nature, so that caterpillars in a stage suitable for parasitism can be found at any time; finally, *Pieris* is very abundant and occurs in concentrated groups, thus exerting a powerful attraction on the parasites.

Cyclical parasitism, says Picard, is not very common in nature, and it does not occur with the parasites of *Pieris*. The percentage destruction by *Apanteles glomeratus* L., for example, oscillates, in the Département de l'Hérault, around 65%. The fecundity of the four principal parasites is indeed sufficient to wipe out the host species, but a small percentage always escapes them, so that it is never quite exterminated. Moreover, the infestation in garden crops is maintained by a continual influx from isolated groups of wild crucifers, which commonly bear unparasitized caterpillars, producing butterflies that return to the cabbage fields owing to the mass attraction exerted by the latter. Moreover, caterpillars continue to develop in the field after the parasites have disappeared.

Cyclical parasitism, according to Picard, implies the existence of a single specific parasite, markedly affected by the variations of the abundance of the host, while the parasites of *Pieris* are multiple and non-specific. Nevertheless, the existence of the parasites is the only thing that saves cabbage crops from destruction by the pierid.

Other important observations were made by Picard. He states that none of the parasites studied by him are able to distinguish parasitized from unparasitized hosts; even in gregarious species like *Pteromalus puparum* L., heavy superparasitism occurs to the marked detriment of the species and it is common also in the "solitary" species.

In 1924, B. Trouvelot described the results of his studies of the potato-tuber

moth, *Phthorimaea operculella* Zell., and its parasite, *Microbracon Johannseni* Vier. He studied the interactions of *Microbracon* and its host under experimental conditions. He brought out the interesting fact that if a female *Microbracon* is placed with the descendants of one female moth, she will only oviposit during about 3 days, and will kill only a small proportion of the hosts, which by the time the next generation of parasites issue, will have reached a numerical superiority which they subsequently maintain; while if the descendants of the moths are given to the parasite at 8-day intervals, in four groups, she will produce descendants in such abundance that the whole of the third generation of the moth will be completely destroyed. The author shows that the curves thus obtained are not exactly like those of the classical cyclical theory. The curves do not fall together at the moment they meet. The host curve begins to fall long before this, the parasite curve long afterwards.

In the laboratories of the United States Bureau of Entomology, field and laboratory studies were carried on in connexion with the parasites of the gipsy and browntail moths, the alfalfa weevil, the European corn-borer, the Japanese beetle, and the small moth-borers of sugar-cane, and other insects, and much valuable information regarding particular problems was accumulated. The papers published by Crossman, Burgess, Collins, Clausen, and others, do not deal to any great extent with general theory, but many of them give very useful data about the course of events in the field and illustrate very forcibly the difficulty of establishing general propositions from the field data it is possible to collect. H. S. Smith and his associates, particularly S. A. Flanders, of the Citrus Experiment Station at Riverside, California, have, however, produced not only outstanding practical successes, but also noteworthy contributions to general theory. Smith published, in 1919, a valuable statement on the points to be considered in the selection of beneficial insects for practical work. In 1929 (1929*a*) he dealt with the question of competition between parasites and showed fairly conclusively that the evidence advanced by Pemberton, Willard and Bissell, for the belief that the introduction of several species of parasites may be injurious because of this interaction, was not conclusive. In 1931 Smith & Flanders published a paper on the egg parasite *Trichogramma*, dealing with the possibilities of utilizing this species in practical control measures. Here they state that the percentage of parasitism by *Trichogramma* tends to vary directly with the host population and, after referring to Chapman's *Tribolium* experiments, they assert as a general biological principle that "within certain limits population density is determined by the nature of the environment" rather than by the number of reproducing parents. "A parasite of the characteristics of *Trichogramma*, which finds its host almost entirely at random, and which has an extremely limited sphere of action", say these authors, "operates in a way very comparable to the operations of a contagious disease; that is, the nucleus of a colony is practically always present, and, given a favourable environment, its abundance in a general way becomes inversely proportional to the distance separating the

individuals of its host species, in other words is determined by the density of the host population." Finally, in 1935, Smith published an important paper on the role of biotic factors in the determination of population densities.

This paper was primarily directed against the view, attributed by Smith to Bodenheimer, that "biotic factors are of little or no importance in bringing about population equilibrium", and that "the introduction of parasites, predators, or diseases from the native habitat of a pest into an area where it has been introduced without them is an unsound procedure".

Smith considers that natural populations oscillate about a mean value which is relatively stable. He asserts that there is always a striking and indeed an *inherent* tendency for the density to swing back to the average, whatever it may be, whenever there is a displacement, either positive or negative, from this average. He notes that changes occur in the average density, and regarded these as "changes in the equilibrium position". The "significant characteristic of population densities from the economic standpoint" is, he says, "the value of the equilibrium position"; and "equilibrium" may be maintenance at a stable population value, or oscillation about a mean.

Smith then studies the logistic or Verhulst-Pearl curve. This curve may be written

$$N=\frac{C\epsilon e^{\epsilon t}}{1+C\lambda e^{\epsilon t}},$$

which is the integral of the differential equation

$$\frac{dN}{dt}=(\epsilon-\lambda N)\,N,$$

where ϵ is the net rate of increase, λ a constant, n the number of individuals in the population and t the time in units. Verhulst (1838) had envisaged the growth of populations as analogous to the fall of a body through a medium made up of layers of greater and greater density; and, as Smith shows, the value given by the curve tends, in the limit ($t=\infty$) to ϵ/λ, which is the value of the population in equilibrium, or at maximum density.

Smith refers to the distinction made by Howard, Fiske and the present writer between general or density-independent and individualized or density-dependent factors of control, and noted that factors of both type are implied in the Verhulst-Pearl formula. The constant ϵ in this formula, represents the effective reproductive rate, when the individuals of the species do not impede their own multiplication, and therefore is the difference between potential reproductive rate and mortality independent of density. Smith also considers the biological significance of the constants on which the asymptotic value of the populations (or, in other words, the population density at equilibrium) depends.

He concludes that "density-dependent mortality factors can determine the average population density or equilibrium position of a species", while "density independent factors acting alone can never do so". He adopts the

view that the controlling effect of climate may increase with density through the effect of competition (p. 894, par. 2), but shows that climatic effects as exhibited in the data put forward by Bodenheimer are not of this type and cannot be advanced as proofs that climate is a true controlling factor. Finally, he agrees with A. J. Nicholson (1933) that "If an attempt be made to assess the relative importance of the various factors known to influence a population, no reliance whatever must be placed on the proportion of animals destroyed by each. Instead, we must find which of the factors are influenced and how they are influenced, and how readily they are influenced, by changes in the density of animals".

The views of Smith are thus, in all essential points, in agreement with those of Nicholson summarized later in this paper. His insistence that climate is a density-dependent factor seems, at first sight, to indicate a divergence. But he explains that its density-dependent action is due "to the existence of protective niches in the environment which are more or less limited in number", "individuals in excess of this number and which cannot therefore attain these niches" being destroyed by unfavourable climate. This appears to agree perfectly with the opinion of Nicholson, that "physical factors that are uninfluenced by the densities of animals cannot control these densities" although "competition forces the surplus animals into unsuitable portions of the environment, where they are destroyed by the physical factors" (1933, pp. 172, 173).

In 1925, Lotka, who had for almost 20 years been working on the application of physico-mathematical concepts to biological problems, published his *Elements of Physical Biology*, summarizing the investigations made in this field by himself and others, and indicating the possible developments in many fields.[1] Population growth is considered by Lotka as a problem of kinetics of which he establishes the fundamental equations, developing from simple assumptions the formula that Verhulst, Pearl and others found to correspond with the growth of animal populations under experimental conditions. In 1923, Lotka had examined the equations published in 1922 by the present writer. He made two objections to the assumptions used: that the generation is taken as a discrete time unit, whereas "it is a very diffuse thing, spread out over varying lengths of time"; that the generation of host and parasite are taken as co-extensive in time; and that the concept of "rate of multiplication per generation" is "not as clear as it might be". He therefore modified the assumptions and produced a pair of differential equations representing the rate of increase of host and parasite respectively. From these he derived curves of a cyclic or periodic character which were either closed curves, indicating a perpetual rise and fall of the two populations, or a spiral, winding around a point of equilibrium, which indicates a "damped oscillation"

[1] The work of Lotka may be consulted in regard to the investigations of Ross, Martini and others on the spread of diseases, which bear on the problems here studied but have not greatly influenced students outside the domain of medicine.

declining toward a stable value. It should be said, however, that Lotka had previously treated a somewhat similar case in a paper published in 1920, and obtained equations of the same form.

Lotka did not attempt to pursue the subject; but some years later his equations were independently developed by the great Italian mathematician, Vito Volterra. The problem of animal interaction had been proposed to him by the Italian biologist, Umberto d'Ancona, who had been led to formulate it by his studies on sea fishing in the upper Adriatic. Volterra immediately realized the interest and importance of the problem; and since he is a mathematician of the first rank, he possessed the equipment required to deal with it. In 1926 he published in the *Memoirs of the Italian Academy of the Lincei*, a comprehensive work of 80 pages conceived on such broad lines that it constitutes a general theory of the population problem.

In this paper Volterra considers the cases of an organism with an unlimited food supply and thus able to increase indefinitely; of two species competing for the same food but differing in their reproductive powers and food requirements; of two species of which one feeds on the other; of n species, competing for the same food, but limited in their increase only by this competition; of n species of which some feed on others, but are limited only by this factor and form associations of odd or even numbers; of fluctuations superimposed on the associations of n species by environmental changes, producing a periodical variation in the coefficients of increase; and of the perturbations produced in an association in the stationary state by the addition of a new species; of n species, forming similar associations, but in which the coefficient of increase of each single species depends on its own numbers—in connexion with which case, Volterra produced a form of the Verhulst-Pearl equation, then, apparently, unknown to him; and of three species of which the first preys on the second and the second on the third (as with a phytophagous insect with primary and secondary parasites).

Many general conclusions were formulated, of which the most important are the following three "laws" concerning the interaction of a predator and its prey:

(1) The fluctuations of the two species (predator and prey) are periodic and the period depends entirely on the coefficients of increase and decrease and on the initial number of individuals of the two species.

(2) The mean numerical values of the populations of the two species are constant, whatever be the initial values of the numbers of the two species, so long as the coefficients of increase and decrease and of attack and defence remain constant.

(3) If we seek to destroy uniformly and in proportion to their numbers, individuals of the two species, the mean value of the population of the prey rises, while the mean value of the population of the predator falls. On the contrary, if the prey is given additional protection, the mean values of the populations of both species increase.

In later papers (listed in the References) the work was extended in various directions. The concept of a delay in the effect produced by the destruction of the prey, on the reproductive rate of the predator, was introduced into the equation for two species; and the differences in the ages and functions of the individuals in the same species was taken into account. A clear and convenient summary of the investigations was published by Volterra and d'Ancona in 1935, in Hermann's *Actualités Scientifiques et Industrielles*. This brief account will make clear the comprehensive character of Volterra's treatment.

On the ground that certain assumptions made during the course of the work are unnecessary and erroneous, and that Volterra himself did not claim to have covered all possible cases, A. J. Nicholson & V. A. Bailey, in a paper published (1935) nine years after Volterra's first work, object to the present writer's assertion (1930) that he had produced an "absolutely general theory of biological associations". No doubt the remark quoted was not literally correct. The writer had indeed said, in an earlier paper, that the method of discontinuous functions is more suitable for the investigations of experimental results, and in a later paper (1931*b*, p. 154) indicated how a formula that neglects age distribution (as do the equations of Lotka and Volterra) may give results in disagreement with the facts. But the two factors of age distribution and delay in the effect produced by feeding on reproduction—which Nicholson & Bailey point out as two of the main defects in Volterra's formulation—though they appear practically automatically in a discontinuous treatment, such as the calculations of Bellevoye and Laurent made forty years ago, and the system produced by the present writer, cannot very conveniently be introduced into formulae obtained by the methods of the infinitesimal calculus by reason of its very nature. To produce an absolutely comprehensive theory is not easy, as we may gather from the remarks of Nicholson himself (1933, pp. 148, 166) in regard to the case of true predators. Nevertheless, when we consider the character of the advance made by Volterra and the developments stimulated by it in the work of authors like Marcel Brélot and V. A. Kostitzin, the present writer's appreciation may not seem to have been excessive.

In 1931, V. A. Bailey published a paper entitled "The interaction between hosts and parasites", in which he studied mathematically as a discontinuous function the problem of random searching of areas for hosts by parasites and produced equations for stable populations, as well as formulae for the numbers of hosts and parasites in the tth generation. He also investigated the same problem "with the limitations to the steady state and concurrent life cycles removed, and with generations and interaction proceeding continuously". He produced a system of differential equations for the general problem of one host and parasite, but did not attempt to solve them; though from them he derived generalized equations for stability of populations from which he deduced that under the conditions stated the density of searching parasites varies inversely as the "areal rate of movement of an average parasite", while the density of

vulnerable hosts exposed to attack varies inversely as the areal rate of the average parasite, "and in other ways depends only on the properties of the parasite". He pointed out that Volterra, in framing his general equations for the problem, assumed that the age distribution of organisms is at all times the same, and asserted that this assumption is, in general, incorrect, and, moreover, is inconsistent with the equations themselves. Two of Bailey's equations closely resemble those of Volterra, but differ from them in that the coefficients they contain are functions of the time and are known only when the whole problem has been solved. In 1933, Bailey (1933*a*) studied the interaction between several species of hosts and parasites, considered as a continuous process. He deduced that stability of populations is in general not even theoretically possible, when there are less parasite species than host species, that when the number of host and parasite species are equal stability can exist, while its possibility depends on the properties of the interacting species if there are more parasite species than host species. He simplified the equations by assuming that the probability of interaction of any host species with any parasite species is independent of the ages of the host individuals (a postulate generally invalid) and studied the behaviour in the "steady state". It is deduced that when only two species interact the steady state is unstable. In the same year Bailey (1933*b*) dealt with non-continuous interaction between hosts and parasites, utilizing the equations produced in 1931. He deduced that the values for host and parasite densities oscillate perpetually above and below their steady values, that when the parasite density passes through its steady value, the host density attains a maximum or minimum value, that the parasite oscillations lag behind the host oscillations by about one-quarter of a period, and that their amplitude increases with time. The period of the oscillation, measured in generations, has a minimum value of 4, and the small oscillations are identical in their character, which depends only on the power of increase of the host.

In 1933 A. J. Nicholson published a paper entitled "The balance of animal populations". In this paper, which is entirely non-mathematical, he endeavours to prove that "animal populations exist in a state of balance", that competition is the only factor capable of producing balance, and that the way in which competition produces balance can be demonstrated, if we start from the assumption that animals search the environment at random for the things they require for existence. Nicholson holds that animal populations, at least, search their environments at random; for though individuals may and do search systematically, the searching by collectivities is unorganized, and therefore random, since the efforts of the individuals composing them are independent, except in certain very rare cases.

If an animal searches the environment at random, the amount of new area discovered as time goes on will progressively diminish according to the law for random distributions (see equation (22)). Giving values to the populations of hosts and parasites, to the rate of increase of the host and to the searching power of the parasite, we can determine under what conditions the populations

of parasites and hosts will remain constant from generation to generation, and the consideration of this situation will allow of certain deductions concerning the effect of varying the factors involved. We can then make the problem more complex by supposing (*a*) that several specific parasites attack a host common to them, (*b*) that several specific hosts are attacked by a parasite common to them, (*c*) that several hosts and parasites interact and (*d*) that hyperparasites intervene, and repeat the investigation of the problems connected with the "steady state".

Let us now suppose that the values of the populations of host and parasite depart from those they had in the "steady state". Such departures from the steady density, says Nicholson, set up "a reaction that tends to cause a return to this density". Interspecific oscillation is thus produced. The nature of the quantitative interrelations and the effect of varying the factors involved is examined. The steady state and interspecific oscillation in predators and their prey are then dealt with, as well as the questions of competition between animals for suitable locations and food, the influence of animal behaviour on populations, and the influence of the physical environment in populations. Two final sections on economic biological control and natural selection conclude the paper.

In 1935 a further paper with the same title, by Nicholson & Bailey, repeats the original conclusions and re-examines the subject with the help of mathematical formulation, introducing a number of subdivisions of the various problems not dealt with in the earlier papers. A final section on continuous interaction is added.

Generally speaking, the reference to the work of other students by Nicholson & Bailey is somewhat negligent and ambiguous, and they do not make much effort to show how their theory is related to the views of their predecessors. The specific characteristics of the theory will be examined in the next section. A few general comments on it may, however, be made at this point.

Here, as in the case of Volterra and d'Ancona, the association between the mathematician and the biologist has been fruitful. We probably do Prof. Bailey no injustice if we say that he might never have thought of engaging in this line of work if its interest and importance had not been pointed out to him by Dr Nicholson. The detailed and orderly *exposé* of the questions treated required a knowledge of entomological facts and literature that a professional mathematician would not easily acquire, though it is necessary if vague but unhelpful generalities are to be avoided. Prof. Bailey has developed, during the course of the investigation, mathematical tools which will certainly be of the greatest value in future studies. One need only refer in this connexion to his 1933 paper on the sequence of values obtained from "recurrence equations" of the type utilized by the present writer in earlier treatments of the problem.

On the other hand, there are one or two curious features in the work of these authors which must be mentioned, since their significance is considerable. Nicholson's investigation seems to have been entirely arithmetical, the

generalized mathematical treatment (called by the authors "mathematical" *tout court*) having been due to Bailey. Since very little quantitative data worth mentioning is available to check the conclusions reached, it is clear that they can only be established as mathematical propositions, and by mathematical methods. Nevertheless, in his 1931 paper, Bailey refers to "Dr Nicholson's belief" that "$N_{2s}(t)$ and $N_{1e}(t)$"—the densities of searching parasites and of vulnerable hosts—are oscillating functions of t, whose amplitudes grow with t. It has not yet, says Bailey, been found possible to establish this conclusion rigorously! This suggests that the mathematician is attributing to the biologist some "inside knowledge" of the problem. But it is impossible to see whence this could be derived, except from a quantitative formulation; and though there are cases in which quantitative relationships, if including the entities specifically designated by the symbols, can be mathematically manipulated and yet are impossible to contemplate intuitively—as in the geometries of Riemann and Lobachewsky—but it is difficult to see how we can have a system that can be the subject of intuitive contemplation and yet brings the expert mathematician to a standstill, in the sense that he cannot get from it, by formal mathematical methods, what intuition discerns.

Furthermore, the 1933 paper by Nicholson is in many ways a very singular piece of work. It has a biological title and it refers continually to the things of nature. The extremely abstract character of language and reasoning, combine, however, to give the paper a staggeringly difficult character, which probably explains why it has evoked so little discussion, in spite of its very wide scope. The abstraction and difficulty of the argument is due, in the opinion of the present writer, simply to the fact that it consists of a *rendering into words of generalization from purely arithmetical reasoning about numbers.* The occasional importation of observational data tends to conceal this fact, as in Conclusion 40, where the irregular distribution of animals "in small groups, the position of which is continually changing," is postulated. But it can be readily established by examining Conclusions 3–10 concerning the "steady state" where one host and one parasite interact. If we take the two equations for the steady state, in the system of Nicholson & Bailey, and make the simple transformations required to express one variable in terms of the others, the conclusions referred to are almost all evident on inspection, and a brief algebraical argument will establish the others. Thus if p = number of parasites, n = number of hosts, and h = power of increase of the host, the "steady state" equation connecting these values is, $p = n(h-1)$. From this it follows that if h decreases so also does p. This is Conclusion 8. Arithmetical calculations would no doubt have been cumbersome; but the author's preference for "verbal reasoning" as opposed to algebraical formulation is difficult to understand except on the hypothesis that he believes he is really talking about nature. Most naturalists using mathematical methods, fall, at times, into this error, or give grounds for the belief that they have done so; but even when they do, the exhibition of the mathematical apparatus gives the reader fair

warning. Volterra, though a mathematician, made the position quite clear when he said (1931 *a*) that "if in what follows we employ a biological *language*, we are in fact engaged in a *purely mathematical* study". Everything in Nicholson's paper suggests a firm conviction that by the methods employed the truth about nature has been discovered; in which case the employment of biological language is quite proper. We need only indicate this viewpoint here. It will be discussed more fully later in this paper.

Raymond Pearl made many contributions to the population problem. His most fundamental advance was probably the rediscovery in 1920 of the logistic curve as a quantitative expression of the combined effect of potential rate of increase and "environmental resistance", though P. F. Verhulst had, unknown to Pearl, worked out the mathematical law concerned in a paper published in 1838.

R. N. Chapman had an important influence on population problems through his text-book *Animal Ecology*, in which the quantitative viewpoint is consistently emphasized. His experimental work on *Tribolium* provided students with a new experimental animal and the technique for dealing with it and has engendered a crop of interesting and valuable studies, among the most important of which are those of the Canadian biologist, John Stanley (1932 *et seq.*). This worker has endeavoured to develop a really accurate mathematical treatment of the problem of the growth of *Tribolium* populations in flour and has produced equations of formidable complexity which make one realize what the intricate problems of nature would involve. The distrust of ready-made, *a priori* solutions, aroused by the study of Stanley's formulae, justify the efforts he has made and clearly indicate the necessity of getting down to facts, but they do not encourage the belief that a workable mathematical formulation is readily obtainable. Stanley's (1934, pp. 728, 729) equation for the number of *Tribolium* eggs in a jar of flour, from the start of the culture to the hatching of the first egg, contains about eighty-six symbols, representing no less than fourteen factors, the last of which is "the quantity of nutrient material which must be injected per unit of time by each adult to maintain the beetle's normal rate of metabolism and provide food for normal egg production".

The work of the Russian zoologist, G. F. Gause, on the growth and interaction of populations of micro-organisms (1931 *et seq.*), has also produced very valuable results. The course of events is rapid, accurate censuses of populations can be taken and, in some cases at least, the nature of the interactions determined by direct observation. The experiments of this author and of many other modern students are summarized in his excellent book *The Struggle for Existence*, in which the relations between mathematical theory and events in nature and the laboratory are admirably discussed. The clear way in which Gause has explained the formation of differential equations suited to various problems makes his book particularly useful to the inexpert mathematician.

B. P. Uvarov and F. S. Bodenheimer have also devoted a great deal of attention to the theory of animal populations. They are perhaps the foremost advocates of the view that climatic factors are mainly responsible for the regulation of the numbers of organisms. Uvarov's work (1931) on "Insects and climate" contains a mass of valuable information on this subject. In one of the concluding sections of this work he deals with the question of "balance in nature", asserting that the comparison of population oscillations with the movements of a pendulum, which tends always to return to a certain position, is "contrary to common sense and amounts to a denial of organic evolution". The analogy must, he says, be corrected by postulating (1) that the oscillations of the pendulum are entirely irregular, and (2) that its point of attachment "fluctuates irregularly and moves with an unequal velocity along an unknown and apparently irregular course". "These corrections, which are absolutely necessary", he concludes, "make the theory of a stable equilibrium in nature and its comparison to a pendulum appear wholly artificial." The key to the problem of balance in nature, he adds, "is to be looked for in the influence of climatic factors on living organisms". It will be clear that Uvarov is here using the word "balance" in a very broad sense. Criticism directed later against his views by Nicholson & Bailey does not appear to take sufficient account of this fact, as we shall show. The views of Bodenheimer have recently been set out in his work *Problems of Animal Ecology* (1938), where a list of his papers will be found. He sums up the matter as follows:

"1. The climatic school was right in pointing out that under normal conditions climate really controls population density in being responsible for the highest degree of destruction. It is, as a rule, the main factor as long as the saturation point of environmental capacity has not yet been approached. This is the normal condition for most animals and even for the longer span of life of species which are inclined to outbreaks. We were wrong to underestimate, in the infancy of our discoveries, the actual part played by biotic factors, especially during the breaking down of gradations.

"2. The biological school was right in making a distinction between density-dependent and density-independent factors. Only the former may be relied upon to bring about the crisis, provided a species in gradation, or in any other way, has approached or surpassed the local specific environmental capacity. Climate may do so, but cannot be relied upon. The school was wrong in limiting biotic factors to the parasite component solely. Parasites are only one of the biotic factors: predators, diseases, effect of population pressure, and lack of food are others. These biotic factors, acting as a whole, will end any outbreak, whereas the single factors are interchangeable. The special stress laid on parasites was unjustified."

Bodenheimer protests against the opinion attributed to him by H. S. Smith (1935) that "the introduction of parasites, predators, or diseases from the native habitat of a pest into an area where it has been introduced without them, is an unsound procedure". The fact that he had himself used parasites for the control of pests in Palestine, should, he considers, "have prevented such conclusions".

On the other hand, the manner in which Bodenheimer refers to the "biological school" of ecologists is equally unjustifiable. His remarks suggest that the general body of workers in biological control constitute the "school" to which he refers and profess the opinions he has criticized. This is not a fact. "The school", says Bodenheimer, "was wrong in limiting biotic factors to the parasitic component solely." The present writer in his 1929 paper on natural control (1929*d*) (section ix) and again in 1930 (1930*a*, p. 59) defined biotic factors in a manner that includes all the elements mentioned by Bodenheimer. He there stated, as does Bodenheimer, that "the control of insect pests is principally effected by the physico-chemical factors, instead of by entomophagous insects". He showed (1928*a*, 1929*d*, 1929*f*) that in nature, when one controlling factor disappears or is diminished in intensity, the effect is automatically reproduced, to a large extent, by other factors, and said (1928*a*, p. 100, 1929*f*) that the real significance of a controlling factor depends "on the fraction of the population for the destruction of which it is *indispensable*", adhering to what Bodenheimer calls "the basic theory of the biological school" ("that an insect increases rapidly in number after having been introduced into a new environment, because the native enemies of the insect have not been introduced and the enemy-component is therefore absent or entirely insufficient") with this proviso. Bodenheimer puts forward in his book the thesis that the European corn-borer is a worse pest in America than in Europe, because the new conditions have enormously increased its vitality. But the present writer had long ago envisaged the possibility that a change of environment might increase the potential reproductive rate (1928*a*, p. 107) and had made (1929*f*, p. 1186), concerning the European corn-borer, the specific suggestion that its destructiveness in America might be due to conditions more favourable to the early stages than those which prevail in Europe. The writer believes that the opinions he has expressed in these matters have the approval of most of those engaged in work on biological control; but it will be amply clear from what has been said that Bodenheimer has no grounds for lumping all these workers in the "school" to which he refers and attributing to them, as a group, the opinions he has criticized.

The study of animal populations in nature has been much stimulated by the work of C. Elton, who now directs the Bureau of Animal Populations at Oxford. Elton's book, *Animal Ecology*, is an extremely valuable survey of a mass of little-known facts. His work and that of his associates has been largely confined to vertebrates and clearly shows how complex the problem of their fluctuations is. The idea, expressed in his book, that animal populations are automatically regulated by natural factors to a position of optimum density, will be examined later.

The investigation of host selection in parasites, which is of fundamental importance in the theory of parasite-host interaction, has achieved very important results through the work of G. Salt, G. C. Ullyett, M. G. Walker, J. Laing, and D. C. Lloyd. G. Salt, while working at Farnham House Laboratory on the parasites of *Cephus pygmaeus* L., the wheat-stem sawfly, carried out an ex-

tensive study on superparasitism in its hymenopterous parasite, *Collyria calcitrator* Grav. He showed that the distribution of the progeny is not in agreement with the hypothesis of random action, but indicates the existence of a power to discriminate between parasitized and unparasitized hosts, to the advantage of the progeny. About the same time he began a quantitative study of the egg parasite *Trichogramma*, and demonstrated that it possesses a similar discriminatory power, which he studied experimentally in detail. Though he thus showed that the parasite selects *individual hosts* in the interests of the offspring, Salt claims that the selection of *kinds of hosts* is not determined by their suitability for its young. His interpretation of his experimental results is thus opposed to the classical notion of instinct, defended by the present writer and H. L. Parker; and his remarks in a general paper on the subject (1938) suggest that he would extend this conclusion to other parasites.[1] J. Laing (1938), who studied the searching activity of *Trichogramma* at the suggestion of Salt, made the important discovery that while the searching of *Trichogramma* in Petri dishes, at a considerable distance from the host egg, appears to be random, it becomes systematic to a high degree, when a host egg has been found. This agrees with the results obtained in the field by Parsons & G. C. Ullyett (1936), who found that eggs of the corn ear-worm attacked by *Trichogramma* tend to occur in local concentrations, showing that the parasite searches intensively in the neighbourhood of the hosts it finds. G. C. Ullyett studied the host selection problem at Farnham Royal in the chalcid, *Microplectron fuscipennis* Zett. He concluded (1936) that the attempt made by Salt to construct a scientific definition of the accepted hosts applicable to all of them has not been successful, and that host selection is a phenomenon of the psychological order. He showed that the parasite is able to discriminate to some extent between parasitized and unparasitized hosts as well as between true and false hosts, and he gave an explanation of the fact that a parasite confined for a long period with a false host will sometimes endeavour to utilize it.

M. G. Walker (1937) re-examined at Farnham Royal the data on *Collyria* used by Salt, and on the basis of a few assumptions, corresponding to the published accounts of host and parasite, constructed a bio-mathematical theory of the action of *Collyria*, giving numerical values in extraordinarily close agreement with the facts. This hypothesis implies a discriminatory faculty, which ceases to operate as the urge to oviposit becomes more intense owing to the lack of hosts and the gradual disappearance of the traces of a previous parasite's visit, through which a new arrival can detect a parasitized host.

The work of D. C. Lloyd (1938) on the egg parasite *Ooencyrtus kuvanae* How., proved the existence in this insect of powers of discrimination and host selection of a still more remarkable character. He showed that the selection

[1] The real point at issue seems to be, whether it is possible to regard the definition of the "typical host" that can be constructed by considering the characteristics common to all true hosts as a *scientific* definition, in that it really includes the causes that induce the parasite to attack. The point is too subtle for discussion in this paper.

of eggs by the parasite can be *directly related to their suitability for the offspring*, other things being equal. He concludes "that the contention that a parasite *generally* 'chooses' as its hosts those which are suitable for the development of its progeny, must be accepted as an observable fact". His data also show that under the experimental conditions utilized the number of eggs a parasite finds is not proportional to the host density, but that *the fraction of the host population found rises as its density diminishes*. He infers from his work that the parasite exhibits a "synthetic relating activity" analogous to psychological phenomena in man.

Having completed the review of the literature of the subject, we may now consider the rational structure of the main theories of population control. After these have been dealt with we shall deal with the mathematical representations of animal interaction that have been constructed and examine their significance. In some cases the theory of animal interaction merely consists in a few postulates used in framing the mathematical system. The theories of Lotka and Volterra are of this character. The prolegomena of Nicholson & Bailey are more amply developed; but here, biological theory and mathematical representation form an indissoluble block, and there is reason to think that these authors do not wish to dissociate them. Nevertheless, for the purpose of this paper it is convenient to do so.

III. GENERAL THEORIES OF NATURAL CONTROL

The most general statement it is possible to frame about natural control is probably that made by R. N. Chapman who said that the numbers of organisms depend on "biotic potential" and "environmental resistance". This amounts to saying that organisms increase as much as they can, which is obviously true, but does not throw much light on the fundamental problems involved. The concept of "environmental resistance", taken over from electrical phenomena, is not altogether adequate as applied to population problems, as will be clear from what follows. Nevertheless, Chapman's formula is not devoid of interest, since it enables one to keep clearly in mind the existence of the two fundamental factors at work—organism and environment; and a study of his writings shows that he has been able to use it in a way that is illuminating and suggestive. Chapman's work on *Tribolium* led him to introduce the idea that some organisms produce resistance to their own biotic potential, though their oviposition rate remains constant; but though he considered that control in such cases is due to "competition", he does not appear to claim that this is invariably the case.

The view expressed by Charles Elton in his book *Animal Ecology* and supported in the Preface to that work by Julian Huxley, is rather peculiar. Elton suggested that organisms tend to maintain a state of optimum density. His remarks indicate that he was thinking of conditions optimum for the *species*; and the comments of Huxley, who wrote that it is important for a species to have "the right enemies", and that in nature "the actual density of population is regulated toward the optimum", support this interpretation.

"It is clear", wrote the present writer (1929*d*) in criticizing this view, "that no such inherent tendency toward an optimum density of population can possibly exist. One reason is, that there is no such thing as an absolute optimum density of population. The density best suited to the species depends on circumstances. When food is abundant, we may have a thriving and healthy population of a thousand individuals for each unit of area; when it is rare, a population of five hundred might produce premature exhaustion of the food supply, having as a consequence the local extermination of the species. But a diminution or increase in the food supply might come about in a great many ways, through the complex action and interaction of a great multitude of diverse causes. In fact, in order to maintain the population of the species at an optimum density, the inherent tendency would have to adjust matters in regard to future contingent events.

"It is therefore quite impossible to admit that organisms possess any instinct or inherent tendency to the maintenance of their populations at a density advantageous to them, or that there are any cosmic mechanisms working to this end. The examples cited by the authors we have mentioned in support of their hypothesis, indeed, demonstrate this clearly. Thus Elton states that a lighthouse keeper in Berlenga Island, off the coast of Portugal, introduced cats to kill off the rabbits, which they did so effectively that they ultimately ate every single rabbit in the island, after which they starved to death.

"There is nothing in this which supports the idea of an inherent tendency toward optimum density. What the example really shows is that organisms multiply without regard to the species as a whole. Whether the rate of multiplication, having regard to natural circumstances, is harmful, indifferent or beneficial to the species is entirely a matter of chance." One should, of course, make an exception for animals living in organized societies, like man and the social insects, which are either subject to intelligent government or exhibit a collective prudence and perspicacity that approaches intelligence. In such species the society attempts to regulate itself to optimum density, though it often fails to do so. It is evident that such auto-regulation cannot be a property of mere agglomerates and that the idea of its existence, outside organized societies, has been reached *by transferring to the species as a whole the powers and tendencies inherent in the individual.* It is fair to state that Charles Elton does not now hold these views, which are mentioned merely for their historical interest.

The present writer, in a paper published in 1929, suggested that the "natural control" of organisms—defined as the check exerted on their multiplication by natural, as opposed to artificial factors—is primarily due, not to any complex cosmic mechanisms or regulating factors, but to *the intrinsic limitations of the organisms themselves.* Every organism has certain specific characteristics, which, though they actually oscillate about a mean, may be considered for practical purposes as fixed; and are so considered in their experiments by ecologists. These specific characteristics imply and indeed include specific needs. An environment which meets these specific needs is,

for a given species, the optimum environment. Given this optimum environment, indefinite increase at a specific rate is possible. But the environmental conditions of the globe vary from point to point and are probably in no two places exactly alike; nor do they remain constant in time. From this it follows that at a given moment, in a given area, the precise environmental complex constituting the optimum for a given species will be found at relatively few points. This is the real reason why organisms, including injurious insects, do not often increase to the point where they become devastating plagues. The fundamental constitution of the universe, composed of a multitude of specifically different and interacting things, living and non-living, necessarily implies a limited possibility of existence for any particular one of them. The fact that there are species, i.e. a variety of essentially limited things, means that their ability to increase is necessarily limited. The world being what it is, *control*, or, in other words, a condition under which an organism *cannot* realize all its potentialities, is therefore *normal* and outbreaks *abnormal*.

An organism is a heterogeneous unit; and if it were inactive, the complex co-ordination of parts characteristic of it would not subsist very long. It would then be in the position of one of those fragile and complicated constructions made by the glass-blower, exposed to the buffetings of the waves on a shingly beach. But the organism is not inactive. The essence of life is movement; but the organism is a material thing and this material engine requires fuel, which it can only obtain from the external world. Moreover, the living organism tends not only to self-perpetuation through its power of nutrition; it tends also to self-expansion, by growth and reproduction.

When conditions in a locality inhabited by a given species approach the optimum, the species automatically increases in numbers, as Malthus and Darwin long ago pointed out. This increase constitutes what we call, technically, an *outbreak*, which is of necessity an *abnormal phenomenon*. The organism considered may continue to increase in numbers for a considerable time, but it obviously cannot go on increasing indefinitely. As it increases in numbers, it necessarily spreads, both in space and time. As it spreads, it necessarily moves to points outside its optimum environment, when its rate of multiplication immediately diminishes. Furthermore, as the population of the species becomes more numerous, the action it exerts on its environment, both indirectly and directly, increases in intensity, producing changes which are, on the whole, in so far as they depend purely and simply on numerical increase, disadvantageous, since they consist to a great extent in the progressive exhaustion of the nutritive power of the environment in relation to the species considered. It must also be remembered that the condition of the globe at any point is never constant. A region which to-day presents conditions optimum for a given species may depart from optimum conditions in the direction X next year and in the direction Y in the following year.

Thus, under even most favourable conditions, there cannot be a continuous and uninterrupted increase in numbers, but simply an oscillating movement

whose amplitude will vary according to circumstances, but is more likely to be feeble than extensive, because of the narrowly circumscribed optimum and restrictive adaptive powers of the majority of species.

Whether the change in the numbers of the species will take the form of an oscillating movement about a mean value, depends, however, on chance. Some species go on increasing for long periods of years. Others, in consequence of environmental conditions producing changes with which they cannot cope, decrease in numbers and disappear completely. Numberless catastrophes of this kind have occurred in the past and, though the majority of them escape notice, still continue to occur. The only reason why oscillation about a mean population value is on the whole more frequent than a steady increase or decrease, is that on account of the great complexity of the natural environment, changes unfavourable to a species do not usually occur simultaneously in all the localities it inhabits, so that although its numbers diminish at one point, they increase at another.

The fact that control may be produced by departures from the optimum in an indefinite number of directions, suggests that the attempt to find specific "limiting factors" or "regulatory agencies" responsible for the control of particular species throughout their range in space and time, is not likely to be successful. Every species has, of course, certain approximately constant characteristics. But while these indicate what environment it *must have to survive*, they do not, except by negation, enable us to define the environment in which it *cannot survive*, since this is *essentially multiple*. This difficulty does not, of course, prevent us from determining the nature and role of the controlling factors acting in a particular case; but it does prevent us from including them in a general definition, since this, by the nature of the case, becomes either too broad or too narrow. The recent careful work of G. M. Stirrett (1938) on the European corn-borer (*Pyrausta nubilalis* Hb.) has provided a striking confirmation of these views. The fluctuations in the populations he studied could be referred to initial moth population, egg production per female, egg survival and larval survival. A decrease in 1929 was due to a fall in moth population and larval survival, in 1930 to a fall in larval survival alone, in 1934 to a fall in moth population and egg survival. He states, also, that temperatures from 59 to 56° F. "not only prohibit flight altogether if they occur early enough in the evening, but prohibit flight whenever they occur in the nightly flight cycle".

What we call "controlling factors" are thus, in general, only the ordinary environmental factors, whose controlling influence depends primarily upon the specific limitations and needs of the organisms upon which they act. If we think too much about parasites and predators, which are, so to speak, *essentially lethal* and *extrinsic*, we are liable to lose sight of this truth; but as soon as we survey the problem as a whole, it immediately reappears.

"The factors of control" form in nature an indissoluble complex. We can, however, regard them as separable for the purpose of classification. As

Howard & Fiske (1911) long ago said, they fall into two great groups, which these authors termed "catastrophic" and "facultative" and which were later (1928*a*) renamed by the present writer "general or independent" and "individualized or dependent". The factors of the first group comprise the *physical forces of the environment* and those *intrinsic defects* in adaptation characteristic of the species;[1] the second group comprises the *predaceous and parasitic organisms*.

The destructive effect of general factors was considered by Howard & Fiske as *independent of the numerical value of the population on which they act*; so that a parasite, for example, destroys about the same proportion of individuals, whether they are scarce or abundant. This view, as the writer (1930*a*, p. 58) pointed out, depends on the assumption that the distribution of individuals with respect to these factors remains unaltered, in spite of increase or decrease in numbers. On this hypothesis they would, of course, be *lethal* factors but not *regulatory* factors. But if increase in population causes an increasingly unfavourable distribution with respect to the physical factors, then they must be regarded as true regulatory factors. We shall return to this point.

Since the physical factors of control "are simply intensities of omnipresent physical and chemical influences above or below the limits between which a given species can subsist", "their distribution, or in other words, the range over which they will be found acting, is obviously far more extensive than that of the biotic factors". It is clear also, that in spite of the interrelations of living things, life as a whole is fundamentally dependent on the inorganic environment; though the inorganic environment could exist without life.

The "individualized or dependent" factors are of course limited in this action by the fact that they are not all-pervading influences, but concrete beings of a certain kind, restricted to spots where the environment is not too distant from the optimum and subsisting for a limited period of time. One of the most important factors in determining the status of parasites and predators is the relative abundance of the food supply, i.e. of their hosts. The more perfectly uniform and continuous the distribution of the hosts, the more likely are the parasites to flourish. Furthermore, since the essential characteristic of the parasite or predator is that it increases *at the expense of its host*, the regions in which the host is abundant are those *in which it is likely to be most effective as a controlling factor*.

The most striking example of this is afforded by the pathogenic organisms, which increase and spread with tremendous rapidity, if the host population has attained a certain density and conditions are otherwise favourable, but disappear almost completely when hosts are scarce and conditions conducive to their health; as is evidenced by the frequency with which epidemics appear

[1] It is, of course, true that the cause of death may usually be referred to extrinsic factors; but in comparing one species with another, their specific limitations must be taken into account, since these affect, in a *general* way, the possibilities of increase (cf. Thompson & Parker, 1928*a*, pp. 15, 16).

in mass cultures of insects in the laboratory, though they may be extremely rare in the field.

If the rate of increase of an enemy does not depend on the abundance of a particular host, then it is clear that its effectiveness will not be correlated with host abundance. This, said Howard & Fiske, is the case with "birds and other predators", which are "not directly affected by the abundance or scarcity of any single item in their varied menu" and "average to destroy a certain gross number of individuals each year"; so that in spite of the fact that birds, for example, tend to destroy "a greater gross number of that species which chances to be the most abundant", the "percentage destroyed will never become greater, much if any, as the insect becomes more common, and, moreover, that after a certain limit in abundance is passed, that percentage will grow rapidly less".

It is evident from the remarks of Howard and Fiske, that the relative independence of the action of such predators as birds, with respect to host abundance, was attributed by them to two things: (1) the non-specificity of their attack, (2) their inability to respond to an increase in host numbers by a rapid increase in their own numbers. Their conclusion, that predators in general are not likely to be effective controlling factors, does not necessarily apply to insect predators, since they, like polyphagous parasites, can increase rapidly in function of host abundance and are, moreover, relatively restricted in their host relations (Thompson, 1929*a*, p. 346).[1]

The fact that the variation in numbers of the larger and more striking elements of a fauna and flora is not obvious and escapes attention, unless it is made the object of special study, gives rise to the idea that their numerical and specific composition is approximately constant over long periods. It seems, indeed, that the populations of a good many species oscillate feebly about a mean value for considerable periods. This gives rise to the idea of the "natural balance" or "natural equilibrium". If we consider, *in vacuo*, so to speak, a pair of organisms, one preying on the other, we can readily see that since the predator increases at the expense of the host, this very increase will eventually tend to exhaust "the nutritive power of the environment" and thus arrest, gradually, or abruptly, the multiplication of the aggressor, and that owing to the fall in the predator population, thus caused, the population of the prey will again begin to increase. A situation of this kind thus exhibits rhythmical or cyclical phenomena which, as F. Picard (1922) suggested, become more marked as the interdependence of predator and prey become more strict. Here, again, we encounter the idea of a balance or equilibrium, analogous to the swinging of a pendulum.

The writer, in common with all others who have dealt with population problems, has commonly used the terms "balance" and "equilibrium". In his 1929 paper on natural control he made certain specific objections to these concepts, and A. J. Nicholson (1933, p. 139) has since classified the views

[1] In regard to birds, see the remarks of H. S. Hanson in *Bull. ent. Res.* **30**, 45. Elton (*Animal Ecology*, p. 119) states that the short-eared owl may have twice as many young in a brood and twice as many broods as usual, during a vole plague, when its food is extremely plentiful.

expressed under the heading of those "put forward as an alternative to what is considered as the untenable hypothesis of balance in nature". However, the writer did not assert, as a general proposition, that the hypothesis of balance in nature is untenable. He said, in the first place, that the use of this term involves reasoning by analogy, which though useful, is dangerous; in the second place, that in so far as it implies the existence of a precise "controlling mechanism" or "limiting factor", "that keeps the species in check over the whole area of distribution", the idea leads to misleading conclusions and should be rejected; and in the third place, that in so far as "equilibrium" implies either stability of population or oscillation about a mean it is not, broadly speaking, what *always* happens, but merely what *sometimes* happens; not a general, but a special case.

"Outbreaks of species", said the writer in the final paragraph of his paper on "Natural control", "are simply due to the fact that conditions momentarily correspond or approximate to the ecological optimum; control means simply a departure in one or many directions from optimum conditions to the point where the species is just able to maintain itself, and below which it decreases in numbers and disappears. The organism with its specific behaviour and requirements is the centre of the problem, and it is not until we understand it that we shall find a clue to the fluctuations in its numbers."

If we attempt to express these views in the language now fashionable we must say that the universe is a *density-dependent factor*. The fact is that the fundamental cause of natural control is neither exclusively *biotic* nor exclusively *abiotic*; it is rather metaphysical or ontological. The fundamental specificity and limitation of beings is its fundamental cause. Attempt to substitute any particular cause for this, and at once a mass of verbal difficulties and pseudo-problems springs up, as we shall see.

In the foregoing discussion the faculty of adaptation, which all organisms possess, has been left in the background, because the very fact that it is a universal possession prevents any particular species from getting any unique advantages from it. Any theory designed to cover concrete cases and real organisms must, however, take account of it; and if, as is commonly believed, adaptation works out as evolution, then we have, both in the individual and in the race, a factor perpetually tending to evade tendencies that make for static balance; as Uvarov has observed. The modifications required to make current theories conform to this idea will be considered later.

In his work "Insects and climate" (1931), B. P. Uvarov devoted a section to the theory of natural control and the idea of balance. He asserts that the "theory of a stable equilibrium in nature is...in direct contradiction to the facts". "While it is true", he says, "that an increase in numbers of a species is usually only temporary, and that a decrease will, sooner or later, follow, there are no proofs that the fluctuations in the two directions are of an approximately equal magnitude, as in the case of a pendulum. Nor is the so-called normal number a constant. We know that some species become more numerous or expand their area of distribution, while others die out. We know

that whole biocoenoses undergo a continuous change, i.e. an ecological succession, which represents only a short phase of the much longer process of geological succession. To speak of a stable equilibrium in nature, and to compare the fluctuations in numbers of organisms with the regular movements of a pendulum, always returning to a so-called 'normal' condition, is contrary to common sense and amounts to a denial or organic evolution. We may compare the course of the existence of a species to a pendulum in motion, but we must introduce two corrections. The first is that the fluctuations of such a pendulum are entirely irregular, both as regards their velocity and their magnitude in either direction. The other correction is that the pendulum is not suspended from a fixed point, but that the point itself both fluctuates irregularly, and moves with an unequal velocity along an unknown and apparently irregular course. These corrections which are absolutely necessary make the theory of a stable equilibrium in nature and its comparison to a pendulum appear wholly artificial." Nevertheless, Uvarov allows that there is a natural balance "resembling that of a cork floating on the surface of a running stream, with its whirlpools, eddies and back currents, while the wind blowing with varying force, now ripples the surface gently, now causes it to rise and fall in great waves. The cork rises and falls with them, comes into collision with other floating objects, now rides on a calm surface and is dried by the sun, now is again rolled over and over by a storm and is beaten by rain, but always continues its journey with an ever-changing velocity and along a fantastically tortuous course." Uvarov concedes the importance of food, natural enemies and biotic factors, but he believes that the key to the problem of the balance of nature "is to be looked for in the influence of climatic factors on living organisms", because climate is "an environmental factor from which there is no escape". Neither the views of Howard & Fiske, nor the paper on natural control by the present writer, are referred to by Uvarov, and though he stresses the importance of climate, he does not explain how increase in number is *controlled* by it, and his remarks suggest that this remains a problem for him.

The work of A. J. Nicholson on animal populations published in 1933, adopts as its fundamental thesis the proposition that animal populations always exist in a state of balance. This is clearly evident, he says, from the fact that the population density of a given species, at a given moment, and in a given place, has a certain definite or determinate value. Some reason why this value is what it is must exist; it must have a cause or complex of causes whose action is exactly what is required to bring it to the point it has attained. Animal populations must therefore "exist in a state of balance, for they are otherwise inexplicable".

To make this evident, Nicholson takes the analogy of a balloon. "A balloon rises until the weight of air displaced exactly balances the weight of the balloon, but if ballast be then discarded the balloon again rises until it reaches a new position of balance. Because a balloon in the air is a balanced system,

there is a relation between the weight it carries and the height it reaches; without balance, the height reached would be indeterminate." Similarly, without balance "the population densities of animals would be indeterminate and so could not bear a relation to anything".

What Nicholson means can best be understood by inverting his argument. If population densities are indeterminate, then they have no definite value. Therefore they have no definite cause, or, are undetermined. But every effect that exists has had a cause proportionate to it. Population densities, since they are definite, must therefore have a cause proportionate to their actual value at any time or place. From this argument Nicholson concludes that balance exists. It is clear, therefore, that by balance he simply means the cause-effect relation. If we agree that this is what is meant by balance then it is indeed evident that balance exists, and that populations exist in a state of balance. But this result has been achieved simply by substituting the concept "in a state of balance" for the concept "caused".

Nicholson then cites the work of Pearl, Chapman, MacLagan and Holdaway, as demonstrating that under experimental conditions organisms in a restricted environment gradually cease to increase in numbers and tend to remain at the population level they reached when the death-rate came to equal the birth-rate. These experiments show, he says, that increasing density "is the essential mechanism for the production of balance in populations". Here the word "balance" is used in a new and quite different sense from that in which Nicholson first employed it; because the mechanism referred to is not merely *causing* the density observed at any given moment, it is also working in such a way as to *regulate* or *govern* the density. "Balance" in the original sense would exist even if the population were increasing indefinitely without limit, while "balance in the second sense means equality of birth-rate and death-rate. It is true that in speaking of Pearl's experiments, Nicholson uses the phrase "stationary balance"; but he does not maintain this very necessary distinction. Indeed, he explicitly rejects the idea that to be in a state of balance animals must "maintain constant population densities". "If a population density is in a state of balance with the environment", he says, "its density must necessarily change in relation to any changes of the environment. A population density that does not change with the environment is evidently not in a state of balance, but is fixed independently of the environment." Nevertheless, almost immediately after this he asserts, against Bodenheimer and Uvarov, that though climate may vary the densities of populations, it does not determine those densities. Climate, he says, "does not possess the property necessary for the production of balance; and it has already been shown that, unless there is balance, population densities are indeterminate and cannot be related to anything". He then asserts that "for the production of balance, it is essential that a controlling factor should act more severely against an average individual when the density of animals is high, and less severely when the density is low".

The argument thus runs as follows: Populations are always in a state of balance, because their values are always determinate and therefore determined. But for the production of balance, it is necessary that the factor involved should act more severely against the average individual when the density of animals is high, and less severely when the density is low. Therefore only factors of this type determine the densities of animal populations, since they alone cause balance.

It is clear that this conclusion has been reached by altering the meaning of the word "balance" in the middle of the argument; and that, though the existence of balance in the first sense has been demonstrated, no proof of balance in the second sense has been provided, excepting the experiments mentioned, and their bearing on events in nature is of course rendered doubtful by the author's own admission that "animals do not maintain constant population densities".

If by balance we mean a state in which the population level remains constant from generation to generation, or an oscillation above and below this value, so that the increase during one period is exactly compensated by decrease during the period following, and if it is proved that this is the balance existing in nature, then it is clear that only factors capable of producing this effect determine population densities in nature. But as we have seen, the existence of balance in this sense has not been demonstrated. Since the balance which is proved to exist is simply the population value, considered as having an adequate cause, then it is obvious that whatever contributes causally to the effect is a real determinant of population density. Nicholson maintains, as we have seen, that climate *varies* population density but does not *determine* it. But to vary the density is to cause a change from one value to another, and, to that extent, to determine it, and thus to determine balance in the sense in which that has been proved to exist.

Nicholson's treatment of the objections made by the present writer and Uvarov, to the concept of balance, is extremely inadequate. He mentions only Uvarov's description of the cork travelling down the river and contents himself with remarking that the cork remains in balance on the water. This implies a return to the first meaning of "balance", whereas Uvarov's analogy was meant to indicate the irregularity of the course of events in nature; but this aspect of the matter is not mentioned by Nicholson, who makes no attempt to deal with the fact mentioned by both the present writer and Uvarov: that balance, either in the sense of stability or in that of oscillations about a mean, is the exception and not the rule. It may be noted, in this connexion, that if we plot on a chart, over a long period of years, the population values of a given species, we can usually, after calculating the mean value for the whole period, show that the yearly values fluctuate up and down around this. But this "mean value" has no objective existence; it is merely the average of a series of what must be called accidental values and has no significance, as establishing the existence of balance in the second sense.

The greater part of Nicholson's paper is devoted to the study of the phenomenon of "balance" in the second sense of the word. It will be clear from what has been said that this cannot be considered as a *general* theory of population densities, because the proof that all populations exist in that kind of balance is invalid. Nevertheless, since it is generally agreed that balance in the sense of stability or oscillation about a mean value is at least approximately realized in nature, it should, of course, be included in any study of the interaction of populations.

Nicholson's views on the "mechanism of balance" in nature do not differ notably from those of previous workers. He accepts their distinction between the mode of action of the physical and biotic factors with the thesis that the former are "density independent", while the latter are "density dependent". The "density dependence" of the biotic factors he considers, following Lotka and Volterra, to be due to *random action*; and he insists very strongly that these factors all be described by the general term "competition". The use of this terminology leads to an unjustifiable rejection of the suggestion made by Bodenheimer, Uvarov, and the present writer, that climate really is a controlling factor. "If increasing pressure of population in favourable areas leads to migration", he writes (1933, pp. 140, 141), "the degree of migration is governed by the severity of competition. The proportion of individuals destroyed by climate is dependent on the proportion competition forces out of the favourable parts of the environment. Therefore, it is competition, not climate, that regulates the fraction of animals destroyed, and so limits the density and holds the population in a state of balance with the environment." Yet suppose we have a region where the edaphic and climatic factors allow the existence of only one tree and that outside the radius of its branches, the insects inhabiting it cannot subsist. When overcrowding occurs, the individuals migrating out of the tree perish as they leave it. Physical factors are at both ends of this process. They have so limited the environment that a very little increase produces starvation or migration; and they actually cause the death of the individuals destroyed. The greater the population in the tree, the greater the proportion of it that will be killed by physical factors. Climate is thus acting as the writer (1930*a*) and H. S. Smith (1935) have pointed out, like a "density-dependent" factor. Here, as elsewhere, there are two elements to be considered: (1) the organism with its fundamental tendency to unlimited self-expansion; and (2) the environment, with its limited capacity for satisfying this tendency. Control is the resultant of these two opposing forces. It is therefore hardly legitimate to isolate one of them and designate it as the sole cause of control. Furthermore, though it is, in a sense, true to say that "competition" between individuals arises *because* of the increase in numbers, yet this increase would not produce any deleterious results if it were not for the character of the environment in which it occurs. The environmental characteristics are thus the actual causes of control.

Nicholson attempts to evade the fact that climate controls organisms by

making a distinction between determination of density and of area of distribution. But every individual may be considered as inhabiting a microclimate; and if half of these are lethal to the species concerned, the area of distribution will be limited, to that extent, by this characteristic, though it is equally true to say that the density has been determined by it.

The word "competition" constantly used by Nicholson, has, moreover, undesirable implications. No doubt there are cases in which organisms do struggle among themselves for food or territory. But if a caterpillar in an isolated plant completely devours its food supply and then dies of starvation, it is difficult to see how this can legitimately be called competition. If a colony of twenty caterpillars comes in the same way to the same end, the case is not notably altered; and even if nineteen die and one more lucky one survives, "competition" still does not seem the right word to use.

It is true that the word is commonly used to designate cases in which the environment is definitely overcrowded. However, everyone who has studied animal populations in the field will agree that there is little obvious evidence of anything that can be called competition. But since it has been claimed on the basis of *a priori* arguments that the regulation of populations can *only* be brought about by some form of competition, it seems necessary to deal with the point a little more fully, though it has been covered in previous papers (cf. 1929*d*, pp. 273, 275; 1930*a*, p. 57; 1931*b*).

The natural control of organisms is fundamentally due to the *intrinsic* limitations of the organisms themselves, and to the fact that at a given moment, in a given area, the precise environmental complex constituting the optimum for a given species will be found at relatively few points. When conditions approach the optimum the organism begins to increase in numbers. As it increases in numbers it necessarily spreads, both in space and time. As it spreads it moves to points outside its optimum environment, when its rate of multiplication immediately diminishes. The discontinuity and variability in habitats, produced by the physical factors both in time and space, is undoubtedly the primary *extrinsic* factor of natural control.

Consider the spread of an organism in time (cf. Auct. 1931).

Ordinarily, the reproductive process extends over a certain period of time. Suppose that for a certain insect it occupies a period of 10 days. The young hatching from the eggs deposited on the tenth day will probably encounter conditions different from those hatching from the first day eggs. If conditions for the larvae of the first batch are optimum, they will probably not be optimum for those of the last batch, because of the progressive changes that occur in the environment, since at every moment in its life history, an organism requires a certain specific habitat.

Moreover, other things being equal, the individuals of the last batch will come to maturity and begin reproducing 10 days later than the individuals of

the first batch. Suppose that d eggs are deposited each day. In the first generation we shall have offspring produced 10 days as follows:

$$G1 = 1d + 1d + 1d + 1d + 1d + 1d + 1d + 1d + 1d + 1d = 10d.$$

In the second generation, as a simple calculation will show, we shall have:

$$G2 = 1d^2 + 2d^2 + 3d^2 + 4d^2 + 5d^2 + 6d^2 + 7d^2 + 8d^2 + 9d^2 + 10d^2 + 9d^2 + 8d^2 + 7d^2 + 6d^2 + 5d^2 + 4d^2 + 3d^2 + 2d^2 + 1d^2 = 100d^2.$$

The reproductive period has thus been automatically extended 9 *days forward.*

Suppose now that the conditions are optimum for the larvae during the first 8 days and lethal from then onwards, the mortality in $G1$ will be 20% and in $G2$ 62%.

Climate is thus working so as to produce the effect of a density-dependent factor, as the organisms spread in time, though absolutely nothing in the way of competition is involved.

The question of spread in space is more complex, since organisms can go only forward in time but backward and forward in space. The essential fact here is that most organisms have different requirements as different periods in their life history. Thus, the larvae of *Pieris brassicae* feeds on cabbage leaves but the adult on the nectar of flowers generally. Now the situations providing the requirements for the adult do not coincide spatially with those providing the requirements of the larvae. Thus, when the adult has moved to the points where it has what it needs for existence, it will probably have moved outside the zones providing the necessities of life for its larva. Since the zones suitable for the larva are limited in number and extent, the natural heterogeneity of the habitat will necessarily cause a spread outward from the zones suitable for it, and when the reproductive stage is reached a large proportion of the adults will be distant from the zones favourable to the larvae. It is clear that though spread from a centre will probably entail some movement inward as well as outward, the proportion of individuals outside the favourable zone will become progressively greater, generation by generation.

To the extent that this occurs, environmental factors in general are working so as to produce the effect of density-dependent factors, as the organisms spread in space, though no true competition may be involved.

In the latter case we may of course expect, in some instances, that actual overcrowding may occur in certain areas. If the requirements of the organism are at all stages practically the same, we shall certainly observe the accumulation of individuals in masses and control caused by the impoverishment of the environment (1929*d*, p. 275). But it is clear that this is, on the whole, a rather uncommon phenomenon, because between one generation and another there is frequently a displacement of the ecological optimum. Thus, the practice of rotation of crops and other circumstances cause displacements of the food plants of many agricultural insects from year to year, and even in the case of insects affecting trees, where the host is long-lived and does not change its

position, the precise conditions for the phytophagous insect will not be maintained at exactly the same points. It will be evident from what has been said that the natural course of events leads to spread in space and time in a manner that inevitably results in natural control, though there may be no competition whatever. We may note that the conditions causing natural control in the field are thus, very often, absolutely different from those causing control in closed environments, and that, for this reason, attempts to apply the Pearl-Verhulst curve to natural populations must be regarded with suspicion, because the equation for this curve implies that the increasing density of the organism progressively restricts its own reproductive rate. Unlike some writers who had used it, D. S. MacLagan (1932*c*) has clearly perceived this point. Natural populations, he says, "automatically check their own increase by virtue of this density effect...when all other factors (biotic and physical) have failed".

It will be noted, therefore, that the explanation here given differs radically from that of Smith (1935) who agrees with Nicholson that climate regulates populations *through competition*.

As we have seen, W. F. Fiske, E. Rabaud and the present writer had examined and developed in various ways the view that the *distribution of progeny in the food material* by organisms is random. This evidence for this view was, and is, that more progeny than can possibly develop satisfactorily with the available food supply are often found on it. Lotka and Volterra developed their equations for the interaction of organisms on the assumption that *the finding of prey* by predators is a completely random process, a supposition which arose not from any extensive study of the biological facts, but rather from the circumstance that it is found in physico-mathematical equations, having to do with encounters between inorganic particles. Nicholson & Bailey adopt the same postulate. It is true, says Nicholson, "that individual animals follow a definite plan when searching"; nevertheless, since these individuals or, at least, groups of them, search independently, "searching within the population is unorganized and therefore random".

In his paper on the random distribution and the parasitic cycle, the present writer showed (1924) that if a parasite distributes x eggs at random among N hosts, the number y of different hosts parasitized is given by the formula

$$y = N\,(1 - e^{-x/N}).$$

This is the basic equation utilized by Nicholson & Bailey.

Let us take an area and suppose that it is divided into N units. The parasites visit x of these units at random, being unable to distinguish those previously visited from those not visited. *The number of units visited at random* is called by Nicholson & Bailey the area traversed. The number of different units visited ($=y$) constitutes the *area covered*.

Suppose now that each area contains a host. The total number of encounters with hosts will be $=x$, while the number of different hosts encountered

will be $=y$. Suppose now that the chance that a parasite will *successfully attack* any host it encounters is $=p$. If p is <1, the parasite will successfully attack less hosts than it encounters. If $p=1$, then it will successfully attack *all* the hosts it encounters. In the latter case we may say that all the area traversed is *effectively traversed*; in the former, only a fraction of it will be *effectively traversed*, since only a fraction of the encounters with host will be successful. *The fraction of the area traversed in which encounters with hosts are successful*—or, to put it in another way, *the proportion of hosts encountered, that is successfully attacked*—is called by Nicholson & Bailey *the area of discovery*. Bailey (1931) had defined it as the *gross effective area traversed by the parasite*. It may be considered as an analogue of *reproductive rate*. The designation of it as an "area" seems to the present writer somewhat misleading.

Nicholson states that if an animal "fails to capture" half the objects of the required kind met with, then the area of discovery is half the area traversed. It is clear that if the animal "captured" the object at the first encounter, it would not be there to be captured at a subsequent visit to the unit of area that had contained it. This might suggest that the area of discovery is half the area traversed when the number of animals *captured* is half the number of animals *present*; or, in other words, that the area of discovery is calculated not from the number of encounters with animals, but from the number of different animals encountered. The way in which the concept is subsequently used shows clearly that the area of discovery is calculated from the number of encounters, as related to the number of units in the area traversed, which shows that the hosts in these units remain available for an indefinite number of visits. It is clear that this concept corresponds to the two "coefficients of attack and defence", γ_1 and γ_2, in the equations of Volterra; and that the idea of an essentially random action is not modified by its introduction.

Nevertheless, there appears to be a certain inconsistency in the remarks of Nicholson & Bailey. In the 1935 joint paper these authors speak of the *areal range* of the animal, defined as the distance it travels multiplied by twice the distance at which it can perceive the object it seeks. The inconsistency lies in the fact that the *areal range* defines a region within which searching for hosts is obviously *not random searching*, since the parasite constantly perceives all the hosts within it and there has not to rely on random encounters. The proviso that it misses a constant fraction of the hosts within the perceptual field does not alter this fact. If we assume that the parasite can perceive objects on every side of itself at a distance greater than the distance it can travel, then so long as there are any hosts within this distance the parasite *will never search for them at random*; if there are no hosts within it the search will be not merely *random*, but useless—a "limiting case". Whenever the hosts are uniformly distributed (an assumption made by Bailey (1931, p. 68)) and *no* farther apart than twice the range of perception, the search for hosts will be constantly non-random. This will be the case for each individual, considered separately. If the parasite cannot detect, until it has visited the host, the fact

that it has been previously attacked, then on the assumption of Nicholson & Bailey we shall have a reduction in reproductive rate through fruitless visits, since the parasite never attacks a host previously visited. On the other hand, a truly random search for hosts will only be obtained, when the distance between hosts is greater than the range of perception.

Thus, the introduction of the concept of "areal range" is inconsistent with the original assumptions made by Nicholson & Bailey, since it brings in a group of cases in which there is no *random searching of areas*, but merely *random visits to hosts*; though in his first paper Bailey expressly states, as we have said, that each parasite searches an area s at random, while the idea of random areal searching is a fundamental point in Nicholson's 1933 paper.

The concept of "areal range" cannot be brought into the formulation adopted by Nicholson & Bailey without introducing a factor for *area traversed*. Thus, taking the equation (30) and supposing that only one parasite is searching, and that all hosts are discovered, we must write

$$1=(1-e^{-s}), \quad \text{i.e.} \quad s=\infty.$$

Thus, the parasite will get *all* the hosts *present* if the area of discovery is equal to the area traversed and this is traversed an infinite number of times.

We can say, in a sense, that by this artifice we have brought in the concept of "areal range". In reality, only its numerical consequences have been brought in and that by means of assumptions that are biologically inadmissible. The concepts of areal range and random searching are therefore irreconcilable.

It should also be noted that Nicholson & Bailey (1935, p. 555) state, as a general thesis, that animals have little difficulty in finding mates, so that this aspect of the matter may be safely neglected. But it is just as important for a parasite to find hosts for its progeny as it is for it to find mates. If it finds mates with no difficulty, whatever their density, why should density so greatly affect its finding of hosts? It seems impossible to accept this reservation.

However, Volterra (1938) has constructed an equation (of the Verhulst-Pearl type, with reversed signs) for the case where reproductive rate is dependent on the finding of mates at random, and this condition could be introduced into the discontinuous system without much difficulty.

IV. THE PROBLEM OF RANDOM SEARCHING

(i) The general question

It will be clear from what has preceded, that the problem of the way in which organisms find the things necessary to their existence or for the perpetuation of their species is of fundamental importance in the discussion of the theories of natural control. Control and a rough balance of nature is maintained because of the enormous mortality among the progeny of all organisms. But is this due, fundamentally and principally, to the fact that organisms "search" for their requirements at random, or to causes of a more

general and deep-rooted character? It seems worth while to consider the question rather carefully.

The nature of random action can best be understood with reference to intentional action, of which random action is the negation, and, in a sense, the derivative.

Intentional action is action that moves toward an end. Everything in nature moves toward an end, being predetermined, in virtue of its nature, to a certain type of action or effect. The peculiar characteristic of living things is that they move toward their *own* ends, this movement being what we call *adaptation*, which is another name for life. But some living things move toward their own ends as *known*, while others exhibit *blind* or *unconscious* adaptiveness. Thus a plant undoubtedly has the power of active adaptation, but we have no reason to think its adaptive movements are conscious. We know, indeed, that we ourselves are the seat of adaptive processes—on the physiological level, for example—that cannot be detected by introspection. The one element in Freudian psychology that will certainly endure is the idea of unconscious psychical or ratiocinative[1] processes, well known to medieval thinkers, but lost sight of by the Cartesians, for whom psychic life and consciousness are co-extensive.

If an organism must, in its own interests, move to an end outside itself, the possibility of success depends on the extent to which its action is governed by *knowledge*. The organism that both knows what it is looking for and recognizes it when it finds it, is better equipped than the organism that merely recognizes the thing sought when it is found. Finally, the organism devoid of any cognitive faculty, so that, as Jennings has said of the Protozoa, it must "prove all things and hold fast to that which is good", is in the worst position of all, since success, for it, depends simply on the possibility of life after passive transference from one point of the environment to another, or after active movement which must be called non-directional, since its course is uninfluenced by the object to be attained. When the movement of an organism is of the last-mentioned type, we can legitimately call it *random movement*, not because it does not move towards an end, because that is impossible, but because it is not being attracted by the object on which its existence, or that of its offspring, depends.

It must, however, be noted that even when the movement of an organism is not directly affected by the object it ought to attain, this object will not necessarily be missed. An organism that is able to search systematically will, at least, not retrace its steps, and its action will thus be less wasteful than true random searching. On the other hand, if the movements of the organism are extensive in relation to the distance separating the suitable objects in the area searched, random action will not necessarily have serious consequences, and cannot be rejected on the ground that it is absolutely incompatible with the

[1] Using this word in a rather loose and inaccurate way, since it does not seem that there can be *true* reason, unless the rational connections in the argument are *seen*.

survival of organisms. In other words, the character of the environment in which random action occurs may be such as to compensate for the non-directional character of this action, considered in itself. Thus in a shower, raindrops may fall over a valley at random and yet all the water is drained away, owing to the topographical and geological features of the region.

A world in which *everything* is random is unthinkable. In fact, no one pretends the world is like that. All agree that it contains some things suitable for a given organism and some things unsuitable for it. G. Salt (1938), in his analysis of host suitability, has clearly shown how many elements enter into this. It is quite certain that the number of things unsuitable for a given organism at a given moment enormously and almost infinitely exceeds the number of things suitable for it. No doubt parasitic insects do not in fact utilize, as hosts for their progeny, all the species in which the latter could develop; but even if they did so, the numbers of suitable hosts would still be almost infinitesimal in relation to the number unsuitable. The use of the word "host" in this connexion is a *petitio principii*, because it tends to restrict the discussion to a certain category of things—caterpillars, for example—of which a high proportion is suitable. When we are considering the general question, we must include under this term all the objects in the environment. As soon as we do this it becomes obvious that the number of unsuitable "hosts" enormously exceeds the number of those suitable. This is the real world in which the real organism searches.

Random action is distinguished from intentional action in that it does not move toward an end. Since living things, in their characteristic vital (or adaptive) activity, move toward their *own* ends, their action may be called random, if it is not directed toward these ends, though it may, and indeed must, attain *some* end. Thus the selection of "hosts" by parasites, though it might not in the strict sense be random, because only objects of certain specific kinds were *in fact* selected, could be legitimately termed random, because there is no definite tendency to the selection of objects suitable for the organism. If the selection were *entirely* random, then we could never make any definite list of the kinds of things selected; if it were random with respect to the interests of the parasite, we could never correlate the categories of "host" and "suitability". In other words, parasite action might be *determinate*, and yet, in a sense, *ateleological*, or *non-adaptive*.

We are, however, enquiring as to the finding of the things that organisms *require*, which is to say the things *suitable for them*, or for their offspring—or, in the case of social animals, their companions. But we may ask, in the first place, whether organisms select the *kinds of things* suitable for them, and, in the second place, whether they select the *individual things* suitable for them. It is evident that to select the *individual thing suitable* is a more difficult feat than to select the *kind of thing suitable*. Nature is composed of *species*; and the individuals belonging to a given species have definite characteristics in common, of whose constancy we can be reasonably certain. Apples *in general* are edible,

and so I am acting reasonably if I eat any apple I come across; that is, I am making an arrangement which is likely to lead to the end envisaged—which is the characteristic of reasonable behaviour. Nevertheless, the precise history and individual peculiarities of the apple may be unknown to me. It may be that the fruit-grower sprayed the apple with lead arsenite, and that through an oversight a lethal dose of this has been left on it. In this event it will turn out, after all, that the apple was unsuitable. Nevertheless, the action remains an essentially reasonable action, since it failed to attain its purpose merely through an *accident*, which is something fully outside the scope of reasonable action. Thus, though a parasite lays its eggs in a caterpillar suitable for the offspring, this intrinsically reasonable behaviour may be frustrated, owing to the fact that an entomologist collects the caterpillar for dissection, or because an insectivorous bird finds it. In a recent and very valuable survey of the problem of host suitability, G. Salt (1938, pp. 241, 242), refers to "the superstition that parasitoids always select hosts that are suitable for their progeny". The "superstition" in question has probably few defenders in scientific circles. It is certain that parasites sometimes do select hosts unsuitable for their progeny, particularly if we define "suitability" not only with reference to the production of fertile offspring, but with reference to all the contingent events that may prevent this either in the first or in succeeding generations. But if we say that they usually select the *kind of thing* suitable for the offspring, we are on pretty safe ground. Tachinid larvae often lay their eggs on geometrid caterpillars closely resembling twigs, but do they commonly lay their eggs on twigs? A tachinid that restricts itself to caterpillars in general is selecting a definite and limited group of things of which a high proportion is suitable, and rejecting an infinite multitude of other things of which the overwhelming majority is unsuitable.

Webber & Schaffner, in their paper on *Compsilura concinnata* Mg. (1926, p. 10), seem to have overlooked this point. Baffled by the enormous variation in the characters of the ninety odd hosts of this parasite in North America, they are led to suggest that "it has no sense of discrimination". But *Compsilura* always attacks insect larvae—generally lepidopterous larvae—and this degree of discrimination restricts it to objects of which the majority are suitable hosts for the offspring. We may note here that the term "tolerance", with which Salt designates the ability of *Trichogramma* to live in different hosts (1938, p. 235), rather begs the question in favour of this author's view that the typical or normal host of a parasite can be scientifically defined in terms of its intrinsic characteristics. Furthermore, the fact that a parasite does not select *all* the kinds of hosts in which its offspring could live, does not alter the significance of the fact that *the hosts it selects* are suitable.

The correct selection of *individual things* involves the avoidance of an indefinite number of practically unpredictable accidents. This is, therefore, a hypothesis impossible to formulate with scientific rigour. Nevertheless, since one important way in which individual hosts are rendered unsuitable for the

progeny of parasites is the accumulation of an excessive number of parasite larvae in or on them, the behaviour of parasites in relation to hosts already attacked by their own or other species enables us, in a sense, to test the ability of the parent to evaluate particular situations in the interest of the offspring. The work of Salt, Ullyett, Walker and Lloyd has shown that the hypothesis of random distribution, adopted by Fiske, Rabaud and the present writer, does not altogether agree with the facts. It is clear that some parasites, at least, distinguish between parasitized and unparasitized hosts and tend to reject the former. The discriminating power possessed by the egg parasite (*Ooencyrtus kuvanae* How.) studied by Lloyd is particularly remarkable, since in the females of this species the tendency to reject parasitized hosts varies in direct relation to their unsuitability for the progeny.

The idea that parasites do not generally select the kind of hosts suitable for the progeny has not hitherto received much attention. Salt (1938, p. 241), who points out the necessity for demonstrating the failure of the selective power in nature, states that he has found, in "a casual search of the literature", some fifty references to this. Not all of the actual cases mentioned are convincing. The observation of Webber & Schaffner (1926) that *Compsilura concinnata* attacks hibernating brown-tail moth caterpillars "year after year", "without the least chance of survival", is not altogether to the point, because the brown-tail moth is, under certain conditions, a quite satisfactory host for *Compsilura*. The authors quoted say that the "same behaviour has been observed in its relation to *Olene basiflava*"; but this assertion is based merely on the finding of a single hibernating *Compsilura* larva in an overwintering caterpillar of *Olene*; and since none of the latter was reared, the fate of the parasite in the hibernating host was never determined. Moreover, if *Compsilura* attacks *Olene* in the spring, its larvae develop successfully on this host; and, on the other hand, as Webber & Schaffner show, the attack on hibernating larvae of some Lepidoptera is successful.

Nevertheless, it is certain that parasites do not invariably select the *kind* of host suitable for this offspring. The reasons for this, as was pointed out in a previous paper (Thompson & Parker, 1927), may be either *intrinsic* or *extrinsic*. A parasite prevented from oviposition by the scarcity of the natural host may be induced, by the physiological urge to dispose of its eggs, to place them in a host it would not normally accept. Again, though the faculty of instinct is remarkably efficient within limits, it is not magical. It operates, we may suppose, in relation to the perceived qualities of the concrete object; it does not penetrate to its inner nature. If we present *Tachina larvarum* L., which is a parasite of the gipsy moth, with an exact, moving imitation of the gipsy moth caterpillar, we may therefore expect the fly to oviposit on it as the practical joker expects his victim to accept the soap chocolate or the explosive cigarette.

G. Salt showed that *Trichogramma* will, in the laboratory, attack unsuitable insect hosts or false hosts of various kinds. For example, it will insert its ovipositor into globules of mercury, will try to insert it into grains of sand and

will actually oviposit in the eggs of *Bruchus*, which are, in general, unsuitable for its progeny and seem irremediably unsuitable, since even after repeated experiments Salt found it impossible to develop a strain of *Trichogramma evanescens* Westw. for which eggs of *Bruchus* constitute satisfactory hosts. Working with *Microplectron fuscipennis*, G. C. Ullyett (1936*a*) found that under certain conditions it will insert the ovipositor into empty gelatine capsules, which somewhat resemble the cocoons of the sawflies which are its natural hosts.

These experiments, of course, confirm the results of previous observers. H. L. Parker and the present writer (1928*b*) when studying host selection in *Pyrausta nubilalis*, found that even when the normal host plant was present, a considerable proportion of the eggs laid by females in cages were deposited on the woodwork and the pots used for the plants. During the breeding of the codling moth carried on for several years by H. T. Rosenberg at Farnham House Laboratory, the routine method was to place the moths in cages lined with paper and having the ends covered with cellophane. Placing apples or apple leaves in the cages did not noticeably improve matters. In these cases, therefore, the insects were certainly putting their eggs on kinds of things entirely unsuitable for the progeny.

Cases of this kind undoubtedly occur on occasion in the field. One of the most remarkable concerns an American tachinid that attacks the browntail moth in Massachusetts. In 1910 from a collection of 24,350 caterpillars, some 276 larvae of this parasite were obtained, indicating an attack over a wide area. All the larvae obtained bore abnormal red spots, and none was able to pupate successfully. The fact that *Coccophagus gurneyi* Comp., according to Compere & Smith (1932), "readily oviposits" in *Pseudococcu scitri* Risso, though it cannot develop in this host, may be another instance of the same sort; but though Salt interprets the statement of Compere & Smith in this sense, the context suggests that they are dealing with the behaviour of the parasites in captivity. The ineffectual attack of the American *Pimpla conquisitor* Say. on the pupa of the gipsy moth, recorded by Howard & Fiske (1911, p. 138) and cited by Salt, concerns, like the first example mentioned in this paragraph, the behaviour of parasites in regard to hosts introduced from another country into the environment of the parasite.

(ii) STUDIES OF FIELD COLLECTED MATERIAL

The thesis that organisms usually select things suitable for themselves or their offspring is difficult to test under natural conditions. It is, of course, merely a subdivision of the general proposition that organisms usually act in their own interests. That organisms *always* act in their own interests is clearly untrue; if they did all organisms would be immortal. Moreover, as we have already shown, in a limited universe such a thing is impossible. That the action of organisms has no positive relation to their own interests is also evidently false. The organism is constantly changing. We may say, in fact, that the

number of its reactions to environmental changes is practically unlimited. If the chance of survival were as high as one-half at each reaction, then the chance that it would live for even a short period would be negligible; it would, as we have said, be like a fragile and complex instrument, left at the mercy of the waves on a shingly beach. But we may consider whether organisms *usually* choose the things suitable for them, or *rarely* do so.

In relation to organisms in general, this matter cannot easily be investigated, because we cannot follow an organism throughout its passive or active displacements, much less a population of organisms. But it can be studied in relation to parasites, and particularly easily in relation to entomophagous parasites. The host of the entomophagous parasite constitutes a small closed environment which can be minutely scrutinized, not only because it is small, but also because it has a structure very convenient for the purpose. As it happens, insects have no connective tissue. Their organs are loosely suspended in a cavity lined with a thin layer of muscles and epithelial cells, and it is very easy to find any foreign object that is in this cavity. Parasites introduced into the cavity and unable to live there may sometimes disintegrate, leaving no trace behind. But this does not generally happen with insect parasites because they are surrounded, in every stage, by an insoluble cuticle, often chitinized or furnished with pigmented spines. Furthermore, parasite eggs and larvae dying in an insect host are very often surrounded by an envelope of phagocytes, and these envelopes do not disintegrate, but persist indefinitely and even increase in thickness, so that they rarely escape the notice of a practised observer.

Those engaged in studying the biology of parasites are obliged to examine with minute care the contents of the insect hosts they dissect, because in many cases it is necessary to find the moult skins of the parasite larvae in order to connect the various developmental stages. This is particularly necessary with tachinid parasites, since the three larval stages are often very different, so that the morphology of one stage bears no obvious relation to that of the next. Many tachinids, moreover, spend only a short time in the first larval stage, and it is often necessary to describe the characters of this from the moult skin, which is often represented only by fragments. The student of this group is therefore obliged to examine his material very carefully and is not likely to overlook anything that does not belong to the normal complement of organs.

For this reason it seems worth while to give, in a condensed form, the results of some of the dissections of insects made by the present writer during the last fifteen or twenty years. It would be easy to extend the list, and almost every student of parasite biology could add to it from his own records.

(*a*) *Crustacea*

From 1917 to 1931 the writer dissected and carefully examined specimens of *Ligia oceanica* L., *Oniscus asellus* L., *Porcellio scaber* Latr., *P. dilatatus* Brandt, *Metoponorthus pruinosus* Brandt, *Cylisticus convexus* De Geer, *Philoscia muscorum* Scop. and *Armadillidium vulgare* Latr., from the British Isles,

France and Switzerland, as well as a lot of undetermined *Porcellio* from Canada. Insect parasites were found only in *Porcellio scaber*, *Oniscus asellus*, *Metoponorthus pruinosus*, and *Armadillidium vulgare*. The *Cercaria* of a trematode were found in *Oniscus asellus* and *Porcellio scaber*; a coccidian was observed in *Porcellio scaber*, *Philoscia muscorum* and *Oniscus asellus*; and echinorynchus larvae, apparently of the same species, in *Porcellio scaber*, *Philoscia muscorum* and *Armadillidium vulgare*. The insect parasites all appear to belong to the rhinophorine group of tachinids. Individuals of some of them occasionally die during the course of the larval development. This occurs most frequently when they attack *Oniscus asellus*, and the author is inclined to think that it is due to the fact that this host frequents damper places than does *Porcellio*. In any event, all the parasites found in the woodlice usually develop successfully in them, and, though all told about 2000 specimens were dissected, not a single stage of any parasite, specifically incapable of living in the woodlice, was ever discovered.

In collecting the woodlice for dissection, lots from different habitats were often mixed together. Moreover, at the time dissections were made it was not always possible to determine every individual parasite, since several of the species are exceedingly similar in the stage (II) most frequently found. The material is therefore not suitable for the study of superparasitism. Nevertheless, although the percentage of hosts parasitized is generally low, amounting on the average to about 11% for *Porcellio* and about 3% for *Oniscus*, more than one parasite larva were sometimes found in one host, though only one ever succeeds in developing, the skin of the dead woodlice being invariably filled by the puparium of the parasite. Thus in a lot of eight *Porcellio scaber* from Farnham Royal, the only parasitized specimen contained three larvae of *Plesina maculata* Fall., two alive and one dead; while of 116 *Porcellio scaber* from Elbeuf, France, 114 were unparasitized, one contained a specimen of *Frauenfeldia rubricosa* Mg., while another contained two specimens of *Styloneuria discrepans* Pand. The fairly frequent occurrence of cases of this kind indicate that these parasites cannot, or do not, discriminate perfectly between parasitized and unparasitized hosts. The adult female could not, of course, do so, since she apparently deposits unhatched eggs in the vicinity of the colonies of woodlice; and the evidence suggests that the larvae cannot make up for this deficiency.

(*b*) *Myriapoda*

From 1915 onwards the writer carried out a study of the parasites of the centipede *Lithobius forficatus* L. Most of the material was collected in the South of England (Cambridgeshire, Suffolk, Hampshire), but some specimens from the environs of Paris were also examined.

Lithobius is an extremely agile and active animal, difficult to capture. It is carnivorous, and as it is protected by an armour of chitinized plates and usually lives under stones or bark or in situations rather difficult of access, it is an unpromising subject for insect parasites. Nevertheless, at least two

tachinids attack it. One is the dexiine tachinid, *Fortisia foeda* Meig., whose biology and larval stages have been briefly described by the present writer (1915). The other is a species still unidentified, found by both J. C. Nielsen and the writer. *Fortisia foeda* deposits larvae, which, if we can judge from their structural characters, go in search of their hosts. The undetermined species, which has a very heavily armoured larva, somewhat resembling that of the American tachinid, *Gymnochaeta alcedo* Loen., may have similar habits, but though the writer has dissected gravid females of many species of tachinids, he has never come across the larva of the *Lithobius* parasite, so that the species may lay undeveloped eggs in the vicinity of the host. We may add that in 1867, E. Newman described the later stages of a hymenopterous parasite of *Lithobius* determined by F. Walker as *Proctotrupes calcar* Hall. The pupae of this parasite were attached to the host in a manner recalling the proctotrupid parasite of wireworms. The writer has never come across this species, but he found on one occasion a *Planidium* (subsequently described by H. L. Parker (1924)), which closely resembled the larva of *Perilampus hyalinus* Say., and is in all probability a chalcidoid of the family Perilampidae. The known facts about this group indicate that the perilampid is a secondary parasite of one of the tachinids. It had entered an unparasitized *Lithobius*, but, as H. S. Smith (1912) showed, this is, with these chalcids, a fairly common occurrence.

Some 300 specimens of *Lithobius forficatus* were dissected during the course of the study and carefully examined for parasites. No parasites other than the two tachinids, which have never been recorded from other hosts and appear to be specific natural enemies of *Lithobius*, were ever discovered, nor were any parasite eggs ever found on the bodies of the specimens examined. On the other hand, though the average parasitism by the tachinids was only about 7·5%, almost half of the parasitized *Lithobius* found contained more than one parasite larva. In the majority of these cases both parasite larvae died, and in only one were both alive at the time of the examination. There is no evidence of discrimination, though the lack of it seems markedly disadvantageous to the parasite.

(*c*) *Insecta*

(*a*) *Collembola*

In 1928 an effort was made to find parasites of the injurious collembolan, *Smynthurus viridis* L., whose ecology was studied at Farnham House by D. S. MacLagan (1932). Many hundreds of specimens, some from the district around Hyères in southern France, and some from the vicinity of Farnham Royal, were carefully examined and dissected; but no traces of any parasites, either external or internal, were ever found.

(*b*) *Orthoptera*

For a good many years the writer studied the parasites of the European earwig (*Forficula auricularia* L.). Two remarkable tachinids, *Digonochaeta setipennis* Mg. and *Rhacodineura antiqua* Mg., attack the earwig. The former

deposits active armoured larvae which go in search of the host; the latter deposits its eggs on the food of the earwig, and the larvae, which hatch in the alimentary canal after the eggs are devoured, pass through the wall of the gut into the body-cavity (*vide* Thompson, 1928*b*). No other insect parasites of the European earwig are known, though nematodes are occasionally found in the body cavity and gregarines commonly occur in the gut.

Material was examined from southern France, northern Italy and the British Isles. In all, several hundred specimens were examined. No parasites, eggs of parasites, or remains of parasites, internal or external, other than those mentioned, were ever found. On a few occasions, two larvae of *Digonochaeta setipennis* occurred in the same earwig, though only one usually emerges from an individual of the host.

(*c*) *Hemiptera*

(i) *Heteroptera*. The heteropterous Hemiptera do not support a large fauna of parasites, at least in the nymphal and adult stages. The Pentatomidae, however, are attacked by the phasiine and ocypterine tachinids. The writer has dissected about a hundred specimens of *Acanthosoma interstinctum*, *Piezedorus literatus* L., and *Rhaphigaster griseus* and found a small proportion of them attached by *Ocyptera brassicaria* F., but never discovered the remains of any other parasites, external or internal. The tachinids mentioned are, of course, specific parasites of these Heteroptera which constitute, for their larvae, the normal environment.

(ii) *Homoptera*. During the course of the work at Farnham Royal, several thousand specimens of the woolly apple aphis, *Eriosoma lanigera* Hausm., have been dissected by members of the staff, including the present writer. On one occasion a larva closely resembling that of *Praon*, which is a normal aphid parasite, was discovered (*vide* Rosenberg, 1934, p. 418). Nothing else but the specific parasite, *Aphelinus mali* Hald., was obtained during the dissections, though *Eriosoma lanigera* is an introduced species, in regard to which "errors of instinct" might be expected, in view of the abundance of the aphid.

In 1914 and 1915 many hundreds of jassids belonging principally to the genus *Typhlocyba*, were dissected and very carefully examined by D. Keilin and the writer. Nothing but Hymenoptera of the dryinid group, Diptera of the family Pipunculidae and Strepsiptera, all of which are known normal parasites of the jassid hosts, was ever discovered. The jassids of the genus *Typhlocyba* contained only the pipunculid *Ateleneura spuria* Mg. and the dryinid *Aphelopus melaleucus* Dalm. Superparasitism very seldom occurred. One might expect the common parasites of aphids to attack the younger stages of jassids, but no evidence of such an attack was ever found.

(*d*) *Coleoptera*

(i) *Galerucella luteola* Müll. The principal parasites of this insect, which is the distinctive elm-leaf beetle, were studied many years ago by F. Silvestri (1909). The writer dissected a large number of specimens from Italy, southern France

and south-western France. The egg parasite *Tetrastichus xanthomelenae*, and the tachinids *Deegeeria collaris* and *Erynnia nitida* were found, the latter species being the most common parasite of the later developmental stages. No traces of any other parasites were found, and there was no evidence that the elm-leaf beetle is ever attacked by anything outside the limited group for which it is a normal host.

(ii) *Hypera punctata* F., and *variabilis* Hbst. These two common weevils have leaf-feeding larvae, which attack clover and lucerne. *H. punctata* usually attacks clover, while *variabilis* prefers lucerne, but both species commonly occur in lucerne fields. Their habits are similar. Both deposit their eggs in a hollow made by the female in the stem of the host plant. The larvae feed in the same situations. The structural differences between the species in the early stages is relatively slight. The cocoons also are very similar, though *punctata* descends into the earth before spinning, while *variabilis* makes its cocoon on the plant or among the debris in the surface of the soil.

In spite of their great similarity these two species have few parasites in common. At least four "egg parasites", of which one, the mymarid *Anaphoidea luna* Gir., is a true internal parasite while the others are really predators, attack the eggs of the weevils. Most of them were found by T. R. Chamberlin (1924) to attack both *punctata* and *variabilis*, but in the experience of the writer are mainly restricted to the latter. Three ichneumonids of the genus *Bathyplectis* and one chalcid of the genus *Tetrastichus*, attack the larvae; of these only one, *Bathyplectis tristis* Grav., is common to the two hosts. Two chalcids attack the prepupae and pupae, but both of these (*Dibrachoides dynastes* Forst. and *Necremnus leucarthros* Nees.) are confined to *variabilis*.

Thus, in spite of the great similarity of the two weevils, in structure and habit, there is a marked difference in the composition of their parasite faunas.

During 1912 and 1913, the writer made an extensive survey of the parasites of *punctata* and *variabilis*, in Italy, France and Switzerland, involving the examination and dissection of thousands of larvae, but did not come across anything abnormal, except on one occasion, when a larva of *variabilis* parasitized by a tachinid (near *Tachina impotens* Rond., *vide* Thompson, 1920) was found. This tachinid completed its larval development in the host, but did not pupate. This, however, is not infrequent with tachinid larvae, which are notoriously difficult to rear. We cannot say that the case represents an "error of instinct".

(*e*) *Diptera*

The writer has not made extensive studies of the parasites of Diptera. He has, however, dissected many hundreds of mycetophilid larvae in an effort to identify a dipterous parasite of *Sciara* originally discovered by D. Keilin. Nematodes and hymenopterous larvae have occasionally been discovered, but there is no evidence that these are anything but normal inhabitants of the mycetophilids.

(*f*) *Lepidoptera*

The work on the parasites of the Lepidoptera carried out by the writer is too extensive to be summarized here. The most thorough and comprehensive study was that undertaken in collaboration with H. L. Parker on the European corn-borer (*Pyrausta nubilalis* Hb.) from 1920 to 1928. The results of the work were published in 1928, and further data were subsequently added by Dr Parker and his associates (1929).

During the course of the study many thousands of specimens in all stages of development, from all the parts of Europe in which the corn-borer exists, were carefully examined and dissected. In one winter alone 10,000 hibernating caterpillars were studied, and this represents only a small fraction of the material collected and reared for parasites. Only two parasites of *P. nubilalis*, doubtfully identified, were known when the work began. By the time it was completed over twenty species, all constantly associated with the host in given localities or generations, and some attacking it over a very wide area, had been discovered and A. Goidanich (1931) has extended the list. The distribution of these parasites is in many ways extremely puzzling, shifting from place to place and from year to year in a way that almost defies analysis.

However, it may be said that during the course of this long study, no evidence of sporadic or non-specific parasitism was found. No parasites or remains of parasites that attack the corn-borer and are yet unable to live in it were discovered. The list of the parasites of *Pyrausta* rose rapidly during the first few years of the work, but after this very slowly. Further investigation sometimes revealed small zones or "pockets", where parasites previously regarded as rare were found in abundance with surprising regularity, but very few additional parasites turned up.

The geographical distribution of the species parasitic on *P. nubilalis* is such that certain of them can never meet in the same host, and consequently can never come into conflict. Generally speaking, several parasites of the same species were more commonly found in the same host than several parasites of different species. In a collection of 468 caterpillars from fields around Auch, Gers, France, dissected and examined in the winter of 1919–20, fifty-six were parasitized by the tachinids *Masicera senilis* Mg. and *Zenillia roseanae* B.B., and the ichneumonids, *Angitia punctoria* Rom. and *Eulimneria crassifemur* Thoms. Only six of the parasitized specimens contained more than one parasite. Two contained two larvae each of *Zenillia roseanae*, one four larvae of this species, one two larvae of *Masicera senilis*, one two dead eggs of *Eulimneria crassifemur* and one five dead eggs of this species. As more than one of the tachinid parasites can develop in a single host some superparasitism is not disadvantageous to them. It will be noted that in none of the hosts examined were parasites of more than one species found.

A study of 230 larvae of the first, or summer generation, in 1920, gave approximately the same results. Sixty-nine (or almost 30%) of the caterpillars

were parasitized by *Eulimneria crassifemur*, two by *Masicera senilis* and four by *Zenillia roseanae*. The hosts infested by the tachinids contained each only one parasite, and none contained more than one species of parasite. The distribution of *Eulimneria crassifemur* was, however, extremely unfavourable to itself. The sixty-nine caterpillars parasitized by this species contained 207 parasite eggs and larvae, that is, enough to destroy 90% of the hosts had they been distributed one to each host, and enough to destroy 60% even if they had been distributed at random. As many as twenty-one eggs of *E. crassifemur* have been found in a single host larvae. In another lot of seventy-one caterpillars attacked by it, 167 eggs were found. It is clear, as was said in a previous paper (Thompson & Parker, 1930, p. 333), that the number of parasites in a single host is much too great to be due to chance. The concentration certainly is not due merely to the fact that many of the hosts are inaccessible, since it is not found in the closely related *Angitia punctoria*; and the habits of *Eulimneria* must be described as inherently wasteful.

As has been said, the fate of the supernumerary larvae is always death, since only one *Eulimneria* issues from the host caterpillar. In fact, however, the extra individuals usually die in an early stage as unhatched eggs, or immediately after hatching. Furthermore, all the eggs and larvae in a group are often found dead, and in a good many cases isolated eggs and first-stage larvae die. Paillot (1924) observed the same thing in a race or variety of *E. crassifemur* attacking the tenthredinid *Neurotoma nemoralis* L., and considered that it is evidence of imperfect adaptation to this host. Since the phenomenon occurs in two very different hosts, it must be regarded as due to an intrinsic weakness of *Eulimneria crassifemur*, and cannot therefore be taken as evidence that this parasite has chosen the wrong host, because in both *Pyrausta* and *Neurotoma* it is apparently a common, widely distributed and successful parasite. On the other hand, its ability to choose the suitable *individual* host is clearly defective, because even if all the larvae in a batch survived for a time, only one can eventually develop.

The fact that parasites of different species have been found less often on the same individual host than parasites of the same species, may be attributed to the fact that they have different ecological optima, or frequent different habitats. This is certainly part of the explanation. But D. C. Lloyd has shown, in his work on *Ooencyrtus kuvanae* How., that this parasite rejects hosts containing hibernating larvae of *Anastatus disparis*, even more decisively than those containing fully developed larvae of its own species; and it may be that other parasites discriminate against hosts parasitized by other species.

It would be possible to prolong almost indefinitely this summary of dissections of field-collected insects. The data assembled are, however, amply sufficient, in the opinion of the writer, to show that insects are in general attacked by a practically constant set of parasites, all of which develop successfully in it, though mortality from extrinsic or intrinsic causes may be considerable at certain stages.

(iii) THE SIGNIFICANCE OF THE FACTS

Let us now consider the significance of this evidence.

It indicates that the choice of the host by the parasite is, in general, both *specific* and *adaptive*. The parasite is restricted to certain kinds of hosts; these kinds are, generally, the kinds suitable for the offspring. On the other hand, under abnormal conditions, as when suitable hosts are scarce, or the parasite is prevented from access to them and allowed only unsuitable hosts at a time when it is ready to oviposit, its behaviour alters, so that it selects hosts not necessarily suitable.

Now, as we have seen, unsuitable or abnormal "hosts" are enormously, indeed almost infinitely, more abundant in nature than suitable or normal hosts. Therefore, if parasites search the environment in general at random, they will be during all but a minute fraction of their lives in contact with unsuitable hosts and with a constantly changing series of host species. The conditions will therefore be such as to cause a breakdown in the restraint and selective power of the parasite. The result of this will be obvious in material collected in the field, which, if the hypothesis is correct, will show, in every species of host examined, (1) many non-viable parasites, (2) host-parasite relations varying indefinitely from point to point and from moment to moment, so that attempts to make a definite catalogue of the parasites of a given host, or of the hosts of a given parasite, will be unsuccessful.

The data given above—and, it may be said, the available data *in general*—are the exact opposite of what they should be, if organisms searched areas absolutely at random. Non-viable parasites are *seldom* met with. The interrelations of parasites and hosts are *specific*. It is true that the parasites of a given host vary in different parts of its range, as do the hosts of a given parasite; but the variation occurs within very narrow limits, and is evidently due simply to the fact that the ecological optima of the host and its parasite always differ somewhat.

The contacts of the organism with the environment are therefore not contacts at random, nor are they unrelated to the interests of the organism and its offspring.

Nevertheless, it is evident that the areas represented by suitable food or hosts are extremely minute in relation to the environmental area as a whole. The area or volume of insect parasites, with which we are chiefly concerned, is also small, sometimes very small. Thus the egg parasite *Trichogramma* is about 0·5 mm. in length. An average egg mass of *Pyrausta nubilalis*, the European corn-borer, may be 3–5 mm. long by 2 or 3 mm. wide. In a moderate infestation there may be only one of such masses on a plant, and only one plant in ten with a mass. The plant may be 2 m. high with seven or eight leaves about 1 m. long and 8–10 cm. across. Suppose the mass has an area of 10 sq. mm. The total leaf surface on such a plant might be 1,600,000 sq. mm. The total surface to be searched in order to find one egg mass would therefore

be 10,600,000 sq. mm. Suppose the *Trichogramma* takes 1 sec. to examine an area of 1 sq. mm. and searches continuously for 24 hr. a day, it will take it 123 days to cover the area containing *one* egg mass of the host. This is obviously ridiculous, and I think the example, absurd though it may seem, shows conclusively that *Trichogramma* certainly does not search the environment for hosts at random, though its small size and fragility may make it peculiarly susceptible to fluctuations in host density, for other reasons. This is an extreme example, yet when we consider the average dimensions of insects, the small size of their hosts in relation to the searchable environment, and the relatively small numbers of both, compared to other objects, it seems abundantly evident that parasites could not search the environment at random and survive.

It is clear, therefore, that some compensating factors must intervene to guide parasites to the food and hosts suitable for them. The first of these is no doubt the arrangement of natural objects in organized assemblages, the second is the perceptive power of the parasite, while the third is the faculty we call instinct, which we may consider merely as a reference to the fact that parasites usually choose suitable hosts. The last-named factor is simply an example of *adaptativeness*, i.e. the ability, characteristic of all living things, to circumvent obstacles in their own interests.

The arrangement of natural objects in organized wholes means that the constitution of nature is the reverse of random. If we consider any specific organism we find that it has specific characteristics, a specific form, structure and physiology. Under certain climatic and edaphic conditions, certain floras tend to develop, and though, as the ecological botanists have shown, the composition of these does not remain constant, yet in a given place and time their composition is approximately specific, and we can establish a fairly definite relation between each organism and the environmental conditions. The insects feeding on plants are like the plants, specific in their form and habits, including their host relations. They tend to be confined not only to certain plant species, or groups of species, but to certain parts of these plants. Some are leaf-feeders, others leaf-miners, some live in buds, some in stems, some in seeds, some under bark and so forth. Thus, provided a parasite, like other organisms, frequents a certain type of environment—which, obviously, *must* be the environment in which the host is found,—its search for the host cannot be altogether random. As G. Salt has said (1935, p. 414): "it is certain that some parasites, and probably that many more, are first attracted not to a particular host but to a particular type of environment. By selecting a particular environment in which to search for hosts, and neglecting other places, the parasite restricts the number of potential host-species that it will meet and so limits the number of species on its list of hosts."

The recently published work of Thorpe & Candle (1939) supports these views. They found that the females of *Pimpla ruficollis* Grav., which had developed in larvae of the pine-shoot moth, are repelled by the odour of pine in the early part of their lives, when they feed on umbelliferous flowers, but

attracted by it when the ovaries are mature and the females ready to attack the pine-shoot moth.

But it is obvious from the examples given above that even in an environment restricted to the host plant of the insect attacked, a parasite could not successfully search at random. There is, in reality, no reason to think parasites do search in this way. The tachinids of the echioomyiine group, which produce very large numbers of heavily armoured larvae, and thus have habits indicating a very high mortality in some stage of development, and might therefore be supposed to distribute their progeny at random, have been found, by J. D. Tothill (1922, p. 55), to deposit their larvae on the leaves and twigs near the web of the host caterpillar (*Hyphantria cunea*). It is evident that this habit affects the chance of survival of an individual larva, but it is also obvious that it is not in any real sense random distribution.

It is, of course, difficult to decide, in any given case, whether the parasite is attracted from a distance directly by the host, or first by the host plant, then by the damaged vegetation, and finally by the host insect itself. H. L. Parker and the present writer (1930, p. 333) noted that the ichneumonid *Eulimneria crassifemur* which attacks the European corn-borer, is aroused to activity by fragments of the corn plant, and explores the material with the ovipositor, if borer larvae have been feeding on it. This suggests that the parasite is first attracted to the host plant and then by successive stages to the host insect. Once the host and parasite are installed in an environment and provided that this does not change rapidly, the task of both the phytophagous insect and its enemy is facilitated, because the parasite, on emerging, is quite likely to find itself in or near a colony of the host. It must also be remembered that organisms are seldom distributed uniformly through the environment. They tend, for obvious reasons, to form colonies, in which mass attraction may exert a powerful influence. F. Picard (1922, p. 107) has pointed out the importance of these factors.

Nevertheless, it seems certain that a parasite can, in fact, detect its host from a considerable distance. A survey of maize fields, made by the writer in north-western Spain in 1925, showed in 4000 stalks, collected from forty fields, an average infestation of about 1·7 corn-borers per hundred stalks; nevertheless, parasitism by *Eulimneria crassifemur* and *Masicera senilis* in the material amounted to approximately 29%. This might, of course, be attributed to a high parasite population in the preceding year, but this could hardly develop except from a large borer population, and the authorities of the maize experiment station in the district had not observed anything of the kind. Moreover, the region has a climate of a markedly maritime character, and, as studies in Great Britain and the maritime regions of France have shown, the corn-borer is permanently scarce in such regions. The relatively high parasitism thus seems to indicate the ability of the parasites concerned to find the host even when it is very scarce, which it certainly could not do if it searched the environment at random.

The common agricultural practice of crop rotation may be regarded, in a sense, as a large-scale experimental test of the thesis that parasites can find their hosts from a distance. This practice entails the removal of the food plant of the phytophagous insect to points more or less distant from those where it must emerge. In spite of this fact, phytophagous insects continue to find their host plants and parasitic insects continue to find their host insects. Organisms are therefore attracted from a distance to the things they require, which is the opposite of random action. The ability of insects to find the things they require at a distance is, moreover, exhibited in a very striking manner by some of the male moths, which, as is well known, will come from almost incredible distances to the females. This example concerns the finding of mates, not food or prey, but it does show that insects do possess the power to detect some of the things they require at great distances.

We may therefore conclude that organisms do not in general search the environment at random for the things they require. We must, of course, recognize that in the phenomenon of seed dispersal the plant is dependent on random action, and it might seem, at first sight, as if the survival of plants dependent on random dispersal affords a proof of the proposition that parasites may survive even though they "search" the environment at random for their hosts. But plants have such a high reproductive power, and are so tolerant of environmental changes, that the environment available to the seeds contains a high proportion of places suitable for them. The fact that random action in plants is compatible with survival has, therefore, no bearing on the case of animals. We may accept the theory of random "searching" as applicable to plants, when due allowance is made in the postulates for the fact that the environment is organized to the plant's advantage. But it remains inacceptable as a theory of *animal* action. It is quite clear that animals do not search the environment at random for the things they require; partly because nature is organized in what we may call a system of sign-posts, corresponding to the perceptive powers of the animal, partly because these perceptive powers establish a positive connexion, which is in some degree independent of distance, between the animal and the thing it seeks. Not only is the searching and choice of environments not random, but, as the experiments discussed above have shown, the searching and choice of hosts is not random either.

Any general theory based on the idea that animal searching is random, is therefore untenable. Such a theory is in fact a theory of the action of *lost animals*; and there is no reason to think it corresponds to events as they really are in nature.

Nicholson & Bailey assert that even if the searching by individual animals is systematic, the searching by the population may still be random, and generally is. This argument may apply to the searching *of areas* in the sense that though one animal may take care never to retrace his steps, or cross his own track, he may cross the track of others of the same species. It may apply also to the searching *of suitable environments*, because the visit of one animal

to an environment may not prevent the visit of another animal to it at a later date. It does not, however, apply to the searching *for* environments. It is evident that if individuals do not search *for* suitable environments at random, then populations do not search *for* them at random either. The general property of non-random action belongs to the population, just as it belongs to the individual.

The theory that the reproductive rate of a predator is a simple function of the ratio between the number of the prey and the area or volume of the environment, has been built up on the postulate that animals search at random. This postulate is erroneous. To say that the reproductive rate of a predator is *absolutely unaffected* by the density of its prey would, of course, be wrong. Beyond certain limits the predator will cease to perceive its prey. If a parasite is led to its insect host by ecological sign-posts, such as a preferred temperature, plant association, evidence of damage and so forth, the absence of these should, theoretically, oblige the insect to search at random. The idea that an insect does *any* searching under such circumstances is, however, questionable. What is most probable is that abnormal conditions will produce abnormal behaviour, whereas a satisfactory theory of animal action can only be constructed on postulates derived from normal behaviour.

It is clear that a theory that makes the chance of survival and the reproductive rate a function of the density of food and prey can be valid only within limits; and that its significance depends on the ratio between the field it covers and the field that ought to be covered. A theory that equates animal action and random action covers, at best, only a fraction of the field. It cannot, therefore, be accepted as a valid general theory.

Nevertheless, the proposition that the natural control of organisms is, in a broad general sense, due to what we may call a "density-dependent factor", appears, as we have already seen (p. 339), to be incontrovertible. This proposition can be deduced from the theory that animals search their environments at random. It seems, therefore, that this theory must be true. This argument is not conclusive, because, though false conclusions cannot be deduced from true premises, true conclusions can, on occasion, be deduced from false premises.

But if it is true, as the present writer has repeatedly maintained, that the mortality on which the natural control of an organism depends, is due simply to departures from the optimum, which differ from point to point over the area inhabited and from season to season and therefore cannot be brought within the compass of an exact definition, then the course of events is a matter of chance, as the writer has explicitly stated (1929, p. 275). But to say that it is a matter of chance is to say that it is a random effect, or an effect of random encounters. However, if control is due to random encounters, then it seems that, in spite of all that has been said, we must admit that the actions of organisms in regard to their environment are, after all, random actions, and we are thus led back to the thesis we have rejected: that organisms search at random for the things they require.

If we say that at every moment in its life history an organism requires a

certain specific set of conditions, departure from which increases the death-rate, then we might describe the attainment of this ecological optimum as the result of a "search", and if we included the interactions that occur *within the organism*, then we should have brought all the activities of the organism under the concept of "searching". Now it is clear that the departure from the conditions required at every moment may occur in an indefinite number of directions, and that the upshot is determined by a great multitude of interacting factors, the precise arrangement of which can only be ascribed to chance.

But this does not prove that organisms act at random. On the contrary, it is absolutely certain that, under such circumstances, random action would instantly be fatal. If I cross a crowded city street when the traffic is at its worst, I may be knocked down and killed by a lorry; this will be an accident, yet I was not acting at random. I had many times crossed the street successfully under the same conditions; and this would never have been possible, if my actions and those of the drivers in the street had been random actions. My death was an accident, because the precise set of conditions determining it was due to chance and not to any cause predetermined to that effect. It was not due to random action on my part, but to the fact, which has already been stressed, that the proportion of suitable situations in the environment was extremely low. As has been said, this proportion is *always* low, and because it is, *organisms die in large numbers, though they do not search at random*; and they die at random because the environment, though not unorganized, varies qualitatively and quantitatively in the details of its structure, from moment to moment and from place to place, in a way that must be ascribed to chance.

It is true, as we have already said, that a completely random universe is impossible. Nature is, in fact, organized, and randomness occurs only within this framework, as a penny can fall only *heads or tails*, though what happens in any given fall is determined by random forces. For this reason we can catalogue and define the *principal* causes of mortality for a given organism in a given environment.

But since the fate of every particular organism at each moment in its career is admittedly dependent on chance, and is in some sense a function of the number of favourable situations, the number of unfavourable situations and the properties of the organism, can we not say, after all, that this principle is the key to the problem of populations? Suppose that a certain organism has, for an interval of time, dt, the natural power of increase $E_1 dt$. In this interval, for N_1 organisms, the increase will be $E_1 N_1 dt$. Call the number of unfavourable situations S; we can say that the number of encounters between organism and unfavourable situations will be proportional to $N_1 S dt$ and equal, say, to $aN_1 S dt$, where a is some suitable constant depending on the exact circumstances. A fraction K of these encounters will be fatal to the organism, whose numbers will diminish by the quantity $KaN_1 S dt$. The rate of increase of the organism will thus be

$$dN_1 = E_1 N_1 dt - KaN_1 S dt,$$

which is one of the fundamental equations of Lotka and Volterra and, written as a discontinuous function, gives the system of Nicholson & Bailey.

The fallacy of this procedure is not immediately obvious; but it is fundamental. Though for particular values of N_1 and S it is possible to define and evaluate the factors K and a, because a certain complex of factors *has* existed and there *has been* a certain ratio between the favourable and unfavourable situations, and a certain percentage of the population *has*, in fact, been eliminated by encounters with unsuitable environments, *yet it is impossible to add up and average these factors from place to place and from moment to moment.* The data are essentially heterogeneous and such data cannot be added up and averaged. We are, of course, dealing with numerical effects, and we can add up the *mortality* stage by stage and get a certain total figure. But this figure has no meaning, because we can get the same mortality through the action of several different sets of causes. It is impossible to get away from the fact that the cause of mortality is *essentially multiple*, definable only as the negation of what is good for the organism and due simply to its *intrinsic limitations.* Owing to this fact we may get the same death-rate for different reasons; since the real causes are different, the numerical identity has no meaning. If one population has a death-rate of 90% owing to frost and the other a death-rate of 90% owing to lack of food, there is no sense in saying that these two populations have the same "searching power", or that the factor Ka is a constant. It is, in fact, radically inconstant.

Moreover, since at every stage in its life history the organism is confronted, in a different way, with the problem of obtaining one of the few suitable environments, it is quite arbitrary, and, indeed, quite wrong to select *one* of these situations and construct on it a comprehensive theory of populations. This, however, is what we do if we make the reproductive rate of an organism fundamentally dependent on the density of its parasites or vice versa. This is equivalent to replacing the general symbol S, representing "unsuitable environments" in the equation given above, by the symbol N_2, representing only parasitic or predaceous organisms. It is clear that the finding of hosts by the parasite is only *one* of the innumerable episodes on which the lives of these two organisms depend. If we consider it *in vacuo*, we can construct a theory of animal interaction which is admirable from the aesthetic standpoint, but this construction has been made possible simply by eliminating the very great part of what really happens in nature. Owing to the mathematical characteristics of the theory, it produces certain results that correspond to facts in nature. Yet it is clear that the phenomena observed in nature do not, and indeed cannot, arise in the manner postulated. In the theory the populations of host and parasite will remain stable, provided the parasite has a certain precise "area of discovery" or "coefficient of attack". In fact, approximately stable populations of host and parasites do exist in nature; but there is no ground for thinking that this relative stability is due to the fact that the values in the equation of the "steady state" are exactly realized in nature.

The criticism just formulated is *fundamental*. If it is accepted, the population theory of Lotka and Volterra, and Nicholson & Bailey, must be regarded as invalid; because some of the factors considered by these authors as constant, or, at least, as varying according to some definite law, are essentially multiple and inconstant, varying in a manner that is fundamentally refractory to mathematical representation, since the values concerned do not follow any definite law, or, in other words, they change in a manner that is fundamentally irregular.

The criticism is merely a restatement of the main theme of the writer's papers on "Natural control": that "the complex of factors which actually effects control in the case of any species differs in composition from point to point and from year to year in the area of distribution". This thesis was not derived from any *a priori* considerations, but from the actual study of the natural control of injurious insects in the field. The extensive study of the control of the European corn-borer carried on from 1920 to 1928, showed quite conclusively that the control of this species in Europe "is not due to any simple cause, but is produced by a complex group of agricultural, meteorological and parasitic factors", and that "the composition of this group of factors is not constant over the whole range of the corn-borer, but varies both qualitatively and quantitatively in the different zones inhabited by the insect, and also, though to a lesser degree, in different years and generations in the same zone" (Thompson & Parker, 1928*a*). D. S. MacLagan, after a careful ecological study of the "Lucerne flea" (*Smynthurus viridis* L.), came to this conclusion (1932*b*, p. 176). The work of G. M. Stirrett (1938), of the Canadian Entomological Service, on the European corn-borer in the Province of Ontario, shows conclusively that even in the same locality the causes actually effecting control do differ qualitatively and quantitatively from season to season. The actual records made by Stirrett concern only loss of eggs, through dislodgement, egg mortality on the plant and larval mortality due to physical factors. But he states that pupal mortality, though not studied, is also a very important factor, as is the variation in the number of eggs laid per female per 100 plants.[1] Taking Stirrett's data, we have constructed a diagram showing the changes in the corn-borer population through the period of his work (Fig. 1). If pupal and adult mortality and variations in reproduction rate had been included in the diagram, the complexity of the facts would be even more evident. Even in regard to the causes of mortality considered, the diagram simplifies to excess. The larval mortality, which is very important and greatest in the early stage, is ascribed by Stirrett to sudden changes in temperature during the period of hatching and establishment, when the tiny caterpillars are attempting to enter the corn plant. No meteorologist would venture to make a long-range prediction in regard to sudden changes in temperature. Here, then, is a factor

[1] This is calculated by Stirrett from the number of females caught in a light trap and the number of eggs found on 100 plants. It varied from a minimum of 2·5 in 1928 to a maximum of 15·2 in 1935.

that is both important and unpredictable; yet unless it can be predicted we cannot evaluate the "coefficient of attack" or "area of discovery" of the corn-borer in the initial stage, because, in all probability, the change in temperature affects the ability of the larva to enter the host plant. But this,

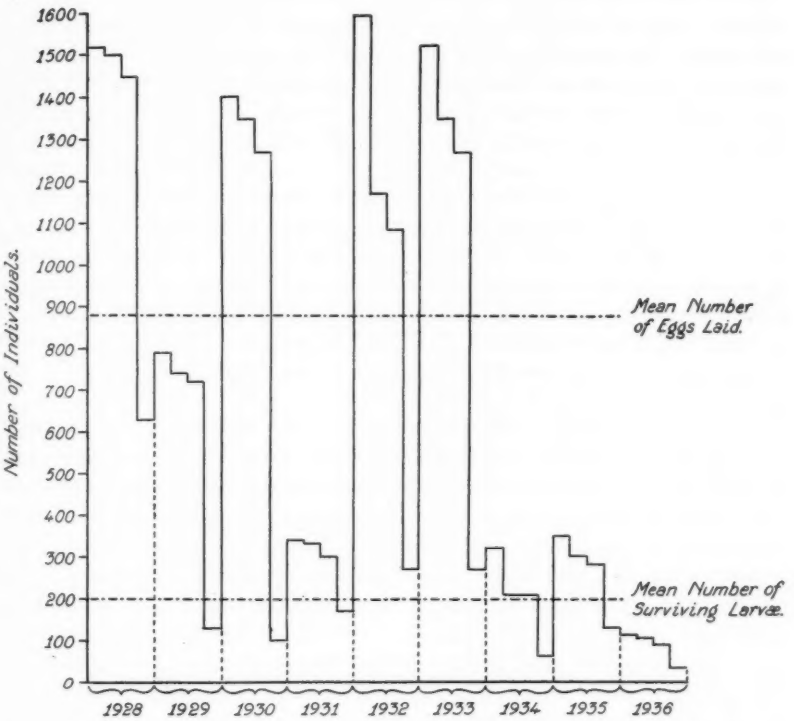

Fig. 1. Variation and mortality in the population of *Pyrausta nubilalis* Hubn., at Chatham, Ontario, from 1928 to 1936, inclusive, plotted from the data of G. M. Stirrett. The upper level for each year represents the number of eggs per hundred plants. The descending steps represent mortality due to detachment of eggs, death in attached eggs, and death in larval stages, all from non-parasitic causes.

though an extremely important episode in the life of *Pyrausta nubilalis*, is only one of the incidents on which its numerical variation depends. It is faced during its career with a series of such problems, and has often several to solve at the same time. Thus the young corn-borer larva, if it is to survive, must get into the plant *and* avoid the attack of parasites. Nicholson & Bailey (1935, p. 554) stress the fact that "the area of discovery of an animal is dependent not only on the properties of this animal, but also upon those of the objects

it seeks". They admit, in consequence, that "any given animal has a different area of discovery for each kind of object it seeks" and realize also that "the value of the area of discovery is influenced by general environmental conditions, such as climate". They think, however, that to avoid complexity in the initial stages of the theoretical investigation, environmental conditions and the "areas of discovery" may be taken as constant. But their subsequent remarks indicate a belief that their assumption has enabled them to reach correct conclusions. The competition that exists between searching animals "is shown", they say, "to produce certain effects, such as balance and interspecific oscillation, which are independent of other environmental factors in their essential features and so must actually exist—unless the fundamental hypotheses given are wrong, or there is some factor capable of nullifying the effects of competition, which seems most improbable". This demonstration depends on the assumption that environmental conditions and areas of discovery are constant. But if, as efficient causes of variations in the numbers of organisms, these factors are radically inconstant, the demonstration is invalid. It is impossible to regard the postulate of constancy as a first approximation to the postulate of inconstancy. If environmental factors and areas of discovery varied according to some definite law, the difficulty might be less serious. But there is no particular reason to think they do.

Another unsatisfactory feature of the "physical" theory of populations is that, generally speaking, it makes reproductive rate a linear function of the ratio between favourable and unfavourable situations. The individual organism is supposed to find a *constant fraction* of these situations; for example, when they become half as common it will find only half the number. As we have already shown, this is an improbable postulate. The fact that animals can perceive things from a distance makes their finding ability to some extent *independent of distance* and therefore *independent of density*. Furthermore, all organisms possess the power of *active adaptation* which is particularly evident in animals. Owing to this power the animal tends to increase its effort as the difficulties of the situation increase. It tends, therefore, to maintain its functions at a certain normal rate, characteristic of its species. Its ability to do so is of course *limited*, but there is good reason to think it is sufficient to compensate for large fluctuations in the density of the things it requires for existence. The more strictly *necessary* these are the more likely it is that the organism will be able to cope with variations in their abundance. The idea that organisms behave in regard to this matter like inorganic particles—which is fundamental to the "physical" theory—is, in any case, one that cannot possibly be accepted without investigation.[1] It is inherently unlikely, and the present writer must say frankly that he believes it to be untrue.

Once again, this is not to say that the reproductive rate of a parasite, for example, is absolutely independent of host density. It is possible to construct a mathematical theory of density dependence, without accepting the postulate

[1] *Vide* J. E. Hardy (1938, p. 11).

of random searching, as will be shown in the next section; and for any given organism under a given set of conditions laws that will hold good can doubtless be formulated, as experiment has shown. But biological theory, experiment and observation are all opposed to the idea that the ability of the organism to find the things it requires to exist and perpetuate itself can be given any fixed value. The adaptive power of the organism, the variation in its physiological processes induced by environmental changes, and correlated with its own development, and the variations in the environment itself, make it impossible to regard this factor as either a qualitative or quantitative constant. Theories constructed on this assumption have, in the opinion of the writer, no relation to reality.

V. THE MATHEMATICAL FORMULATION OF THE INTERACTION OF POPULATIONS

Having considered the general problem of natural control we can now examine the attempts made to deal with animal interaction mathematically. For the purpose of this paper only the basic methods and assumptions need be considered.

The methods used by the present writer were developed in connexion with the biological control of insect pests. The object of the work was not, primarily, the construction of a valid general theory of animal interaction or natural control, but rather the development of a method of analysis that might be helpful in experimental studies and practical problems. The assumptions made in the initial papers were not regarded as axioms. They were, in fact, altered repeatedly during the course of the investigation. The theory of natural control was dealt with from the biological and not from the mathematical angle, as has been shown in the preceding section; and the solution proposed was formulated in biological, not in mathematical terms.

The first case dealt with was that of a population comprising an insect parasite and its insect host. The assumptions underlying the treatment are as follows: the insect host reproduces indefinitely at a constant rate, if not attacked by the parasite; the parasite reproduces at the expense of the host at a constant rate; the sex ratios of host and parasite have fixed values; each parasite lays one egg in each host attacked and attacks only unparasitized hosts; all hosts are at all times available to attack, unless already parasitized; the generations of host and parasite are synchronous; but within each species they are discrete, in other words, do not overlap.

Putting the initial number of hosts $=n$, the initial number of parasites $=p$, the reproductive rate of the host per generation $=h$, and the reproductive rate of the parasite $=s$, and assuming, for the sake of simplicity that both species are parthenogenetic, female-producing insects (though symbols for sex ratios were actually introduced in the initial paper), we proceed as follows:

In the first generation we have

$$n_1 = n \times h = nh \quad \text{hosts}$$

$$p_1 = p \times s = ps \quad \text{parasites,}$$

each of which destroys one host, so that the number of hosts emerging is

$$nh - ps.$$

In the second generation we have, therefore

$$n_2 = (nh - ps) \times h = nh^2 - psh \quad \text{hosts}$$

$$p_2 = ps \times s \qquad = ps^2 \qquad \text{parasites,}$$

each of which destroys one host, so that the number of hosts emerging is

$$nh^2 - psh - ps^2.$$

In general, the number of hosts and parasites emerging at the *end* of the tth generation may be written

$$n_t = (nh^t - psh^{t-1} - ps^2h^{t-2} \ldots \text{ to } (t+1) \text{ terms}), \tag{1}$$

$$p_t = ps^t, \tag{2}$$

The expression for n_t is, with the exception of its first term, a geometrical progression, and may be written

$$n_t = nh^t - ps\left(\frac{s^t - h^t}{s - h}\right). \tag{3}$$

If we have $s = h$, the equations (1) and (2) become

$$n_t = nh^t - tph^t, \tag{4}$$

$$p_t = ph^t. \tag{5}$$

From these equations we can easily derive the number of generations required for the extermination of the host by its parasites, since this will have occurred when n_t is $=$ or < 0.

If the reproductive rates of host and parasite are equal, we have from (4)

$$t = \frac{n}{p}. \tag{6}$$

Otherwise, we can write $s = ah$, where $a \neq 1$, and by substitution in (3) we derive

$$t = \frac{\log\left\{\dfrac{na - n + pa}{pa}\right\}}{\log a}, \tag{7}$$

from which

$$t = \frac{\log\left\{\dfrac{ns - nh + ps}{ps}\right\}}{\log s - \log h}. \tag{8}$$

If we have $s \geqslant h$, there is always a real value of t for which n_t becomes equal to or less than 0; if we have $s < h$, the necessary condition for a real finite value of t is

$$\frac{p}{n} > \frac{h-s}{s}, \tag{9}$$

though the values of n_t and p_t increase for all values of h and $s > 1$.

In the particular case when

$$\frac{p}{n} = \frac{h-s}{s}, \tag{10}$$

$t = \infty$, i.e. the parasite and the host populations are increasing in the same proportions and one will never overtake the other.

If, in addition, $s = 1$, then

$$p = n\,(h-1), \tag{11}$$

and the populations are stabilized, the numbers of host and parasite remaining constant from generation to generation.

The foregoing equations are based, as has been said, on the assumption that parasites choose *only unparasitized hosts*. But there are parasites that habitually deposit many eggs, all producing progeny, in a single host individual. Furthermore, in the case of predators, we have mobile larvae each of which may destroy many hosts during the course of its life.

Suppose, then, that *more* or *less than* one larva is required to destroy one host and that the number required for this purpose $= m$.

If the reproductive rates of host and parasite are equal, the time required for control is

$$t = \frac{mn}{p}, \tag{12}$$

while if we have $s >$ or $< h$, so that $s = ah$, the time required is

$$t = \frac{\log\left\{\dfrac{mn\,(a-1)+pa}{pa}\right\}}{\log a}, \tag{13}$$

from which

$$t = \frac{\log\left\{\dfrac{mn\,(s-h)+ps}{ps}\right\}}{\log s - \log h}. \tag{14}$$

If we have $s > h$, there is, as in the preceding example, always a real finite value of t for which n_t becomes equal to or less than 0; if we have $s < h$, the necessary condition for a real finite value of t is

$$\frac{p}{mn} > \frac{h-s}{s}, \tag{15}$$

though, as before, the values of n_t and p_t increase for all values of h and $s > 1$. When we have

$$\frac{p}{mn} = \frac{h-s}{s}, \tag{16}$$

the two species both increase indefinitely; and when we have

$$\left.\begin{aligned} s &= 1, \\ p &= mn\,(h-1), \end{aligned}\right\} \tag{17}$$

the populations are stabilized.

Hitherto, the reproductive rate of the parasite has been taken as constant. It may, however, be taken as varying in some definite manner, owing to causes either extrinsic (various environmental factors) or intrinsic (appertaining to the behaviour or physiology of the parasite). The reproductive rate of the host may also vary, from causes other than parasitic attack. Finally, these variations might occur in both host and parasite.

Thus, into the complex of n individuals of a host species with reproductive rate $=h$, and p individuals of a parasite species with a reproductive rate $=s$, we could introduce q individuals of a secondary parasite with a reproductive rate $=r$. The presence of the secondary parasite would obviously affect the rate of increase of the primary parasite and thus the rate of increase of the host. We could bring in the idea that agricultural methods destroy a certain proportion of hosts and parasites in every generation during the developmental period. We could suppose that the generations of hosts and parasites do not synchronize one species having more generations per annum than the other.

We might also postulate that the reproductive rate of the parasite is in some sense a function of the number of hosts available. This case is worth considering more closely. Suppose that in every generation a constant fraction i of the host population is, for some reason, inaccessible to the parasite, the accessible fraction being a; $(a+i=1)$. If parasites choose unattacked hosts until there are no more available and then oviposit in parasitized hosts; and if one parasite issues from each host attacked, the number of hosts and parasites emerging in the tth generation is given by the equations

$$n_t = nh^t i^t, \tag{18}$$

$$p_t = nh^t i^{t-1} a. \tag{19}$$

If we have $hi > 1$, then the value of n_t will continue to rise; if $hi = 1$, then the populations of host and parasite will remain stable, at the values n and na; if we have $hi < 1$, then n_t will tend to 0 as the value of t increases.

If we say that the reproductive rate of the parasite, which depends on its encounters with the host, is a function of the numerical ratio between host and parasite populations (Thompson, 1923*b*, pp. 194, 195; 1930*a*, p. 67), we may suppose that when the number of hosts is $=n$, the number of parasites is $=p$, and the dimensions of the area containing them, in conventional units, is $=A$, the number P of parasites finding hosts is indicated by the relation

$$P \propto \frac{pn}{A}.$$

It is evident that the larger the area, for given numbers of hosts and parasites, the smaller the number of parasites finding hosts, if their distribution is uniform; on the other hand, in a definite area the probability of encounter and, consequently, the value of P, will rise as the number of hosts and/or parasites rises and fall as it falls.

If we wish to evaluate the change produced by an alteration in the numbers of the host, suppose the number changes from n to n_1, P will then become P_1. The relation between the numbers of parasites finding hosts will then be

$$\frac{P_1}{P} \propto \frac{kn_1p}{A} \div \frac{knp}{A}, \quad \text{i.e.} \propto \frac{n_1}{n}.$$

We may therefore write

$$\frac{P_1}{P} = \frac{kn_1}{n},$$

where k is a constant, whose value depends on the species.

Now since P_1 designates hosts found, and a parasite oviposits when it finds a host, we may say that P_1 designates reproduction; and since the parasite populations have been taken as constant ($=p$) we may say that the ratio P_1/P represents the relation between *reproductive rates* when the value of the ratio between host populations is kn_1/n. Thus, if s is the reproductive rate when there are n hosts, the reproductive rate s_1, when there are n_1 hosts, will be

$$s_1 = \frac{kn_1s}{n},$$

or, writing

$$K = \frac{ks}{n},$$

$$s_1 = Kn_1.$$

The relations between successive generations of host and parasite would then be given by the equation

$$n_{t+1} = n_t h - p_t K n_t, \tag{20}$$

$$p_{t+1} = p_t K n_t. \tag{21}$$

In this system the reproductive rate of the parasite rises as host numbers rise, and falls as host numbers fall. It could be complicated by the additional postulate that host reproductive rate rises as host numbers fall, because the rarefaction of the host population has made more places available for the offspring.

Up to the present it has been assumed that the parasite can and does choose unparasitized hosts in which to oviposit, except in the development of equations (12) to (17) which included gregarious parasites and (18) and (19) where the parasite was assumed to lay in parasitized hosts when no unparasitized specimens were available.

Let us now assume that the parasite cannot, or at least does not, choose between parasitized and unparasitized hosts. Consider a parasite laying its eggs in a group of 100 caterpillars, all originally unparasitized. When the first

egg is deposited there are 1 parasitized caterpillar and 99 unparasitized. If the parasite can and does choose only unparasitized hosts, the deposition of a second egg will certainly give another parasitized caterpillar. If not, then the probable result of the action will depend entirely on the numerical relation between parasitized and unparasitized. Clearly, there will be 1 chance in 100 that a parasitized caterpillar is selected at the second oviposition and 99 chances in 100 that an unparasitized caterpillar is selected. The *probable number* of caterpillars parasitized by the second egg would therefore be $(0{\cdot}99 \times 1) = 0{\cdot}99$; and the probable number unparasitized is, therefore, 98·01 and the probable parasitism by the third egg $(0{\cdot}9801 \times 1) = 0{\cdot}9801$, so that, when three eggs are deposited, the probable total parasitism is

$$(1{\cdot}99 + 0{\cdot}9801) = 2{\cdot}9701.$$

It is thus clear that the results obtained by the addition of a parasitized egg to the host population depends on the relation between the hosts still unparasitized and the total population, when the addition is made.

Suppose that when x eggs have been deposited there are N hosts and $(N-y)$ of them still unparasitized. Suppose that the number N is very large. If then we have an addition Δx of eggs so that Δx is very small in relation to N, we may assume that the additional increment of parasitism Δy is given by the equation

$$\Delta y = \Delta x \frac{N-y}{N}.$$

The relation between the increments of x and y is therefore given by the differential equation

$$\frac{dx}{N} = \frac{dy}{N-y},$$

from which, integrating, we obtain

$$y = N\,(1 - e^{-x/N}), \tag{22}$$

where y is the number of parasitized hosts obtained by the distribution of x eggs at random among N hosts, on the assumption that the number N is very large, and e is the base of the Napierian logarithms and $= 2{\cdot}7128\ldots$. It will be noted that here, as in the preceding numerical treatment, the result of increments of oviposition depends *entirely* on the numerical relation between the parasitized and unparasitized parts of the population. The oviposition itself is therefore at all times *non-directional*, which is to say, *random*, with respect to the different types of hosts available.

Returning now to the first example in this section, where we have ps parasitized eggs distributed among nh hosts, it is evident that the number of parasitized hosts will not be ps, but

$$nh\,(1 - e^{-ps/nh}),$$

while the number of unparasitized hosts will be

$$nh - nh(1 - e^{-ps/nh}), \quad \text{or} \quad nhe^{-ps/nh}.$$

To simplify write

$$\mu = \frac{ps}{nh}.$$

The number of hosts issuing at the end of the $(t+1)$th generation is then

$$n_{t+1}=n_t h e^{-\mu}. \tag{23}$$

If no parasites die owing to the fact that they share a host with others, the number of parasites issuing at the end of the $(t+1)$th generation is

$$p_{t+1}=ps^{t+1}. \tag{24}$$

The equation for n_{t+1} is like (18) and (19), a "recurrence equation", where the value of each generation must be calculated from that of the preceding generation, while the equation for p_{t+1} is of the ordinary type.

From these equations the conditions for stability of population are easily deduced: they are given by the equations

$$\left.\begin{aligned} s&=1, \\ p&=nh \log h. \end{aligned}\right\} \tag{25}$$

If only *one* parasite issues from each host attacked then it is clear that the number of parasites emerging in a given generation will be the same as the number of hosts attacked. The equations for n and p will therefore be

$$n_{t+1}=n_t h e^{-\mu_t}, \tag{26}$$

$$p_{t+1}=n_t h\,(1-e^{-\mu_t}), \tag{27}$$

and in this case the equations for stability of populations are

$$\left.\begin{aligned} s&=\frac{h \log h}{h-1}, \\ p&=n\,(h-1). \end{aligned}\right\} \tag{28}$$

We may note that in the latter case, as in all those where superparasitism produces mortality, the reproductive rate of the parasite will be affected by the random distribution of the progeny, the results of which will depend, in turn, on the ratio between number of hosts and number of parasites. Thus from (22) we can see that if a parasite distributes 100 eggs at random in 100 hosts, it will produce 63 offspring, whereas, if it distributes them among 1000 hosts, it will produce 95 offspring. Thus, supposing the area of distribution to be the same, high host density causes reproductive rate to rise, while low host density causes it to fall.

The situation where a fixed proportion of the host population is inaccessible to attack (equations (18) and (19)) can also be modified by assuming that the parasite distributes its progeny among the accessible host population *at random*. In this case we have $p_t s$ parasites distributed among $n_t ha$ hosts. Therefore

$$n_{t+1}=n_t h\,(i+ae^{-p_t s/n_t ha}) \tag{29}$$

$$p_{t+1}=n_t ha\,(1-e^{-p_t s/n_t ha}) \tag{30}$$

If $h=1$, n_{t+1} and p_{t+1} tend, asymptotically, to 0; if $h>1$, n tends, asymptotically, to the value of $n_t hi$, while p tends to the value of $n_t ha$. If hi is $=$ or >1, then the value of n increases. If we have

$$\left.\begin{aligned} s &= \frac{nha}{p}\log\left(\frac{ah}{1-hi}\right), \\ p &= nhae^{-ps/nha} \end{aligned}\right\} \qquad (31)$$

and $hi<1$,

the population remain stable. If hi were $>$ or $=1$, then the population of inaccessible hosts would be $>n$ or $=n$. Even if it were only $=n$, it is clear that the host population could not remain stable, because the accessible host population would always have a positive value unless the index of e were infinitely large, which would require an infinitely large parasite population.

Equations (20) and (21) cover the case where the reproductive rate of the parasite depends on the numerical ratio between the populations of host and parasite. In developing these equations it was shown that if s is the reproductive rate of the parasite when there are n hosts, the reproductive rate s_1 when there are n_1 hosts will be

$$s_1 = Kn_1, \quad \text{where} \quad K=\frac{ks}{n}.$$

It was assumed that the Kn_1 progeny were distributed among the unparasitized hosts; but one might postulate that the distribution is made at random. Suppose, then, that p_1 parasites with an average reproductive rate of Kn_1 distribute their progeny at random among n_1 hosts, the number of hosts parasitized will be

$$n_1\left(1-e^{-kpn_1/n_1}\right)$$

or

$$n_1\left(1-e^{-kp_1}\right).$$

The equations for the numbers of hosts and parasites in the successive generations will then be, on the assumption that only one parasite issues from each host attacked,

$$n_{t+1} = n_t h e^{-kp_t}, \qquad (32)$$

$$p_{t+1} = n_t h\left(1-e^{-kp_t}\right), \qquad (33)$$

and the equations for stable populations derived from these will be

$$\left.\begin{aligned} K &= \frac{\log h}{n(h-1)}, \\ p &= n(h-1). \end{aligned}\right\} \qquad (34)$$

This is the system adopted by Nicholson & Bailey as the basis of their theory of natural control. They derive it from the thesis that animals search their environments at random.

Suppose that in an area of U units, p parasites each examine at random m units. Then pm is the total number of examinations of units and the number N of *different* units examined, is given by

$$N = U\left(1-e^{-pm/u}\right).$$

In this equation $1/u$ represents the fraction of the total area *covered* by an individual parasite by the examination of 1 unit, while m/u is the fraction of the total area traversed by an individual parasite in its lifetime, and N/u the fraction of the total area covered by all p parasites, searching the environment at random.

It is clear that the fraction of the host population the parasites will secure (counting only *different* hosts) depends on the fraction of the total area they *cover*. If we write $s = m/u$, the number of a population of nh hosts killed by the parasites will therefore be

$$H(p) = nh(1 - e^{-ps}), \tag{35}$$

and the number escaping

$$H(e) = nhe^{-ps}, \tag{36}$$

the recurrence relations for the successive generations being of the form already given. It may be noted that in developing his equations Bailey (1931) assumed that though a parasite may visit a host more than once, it does not attack it more than once; which gives the same result as the assumption that though the parasite attacks the host at each visit, only one offspring survives in each host attacked.

It is evident, from what has been said, that we can obtain a formula relating parasite reproductive rate to host density without specifically postulating that the parasite searches the environment at random. Thus we can say, to begin with, that each parasite visits at random a constant fraction of the host population, whatever be the number of hosts, without specifying how this comes about, and that these fractions are superimposed at random.

But we can also suppose that, though all hosts in the area are at all times perceived and every one, considered separately, accessible, the number actually visited depends on their density, simply because the time and energy for travelling from one to another is limited. Thus, I may hope to visit ten shops in an afternoon, may know exactly where they are and how to get to them, so that there is nothing random in my actions. Yet I may be able to visit all the ten shops if they are within a radius of a mile and only five of them if they are on the edge of a circle two miles in radius. These two hypotheses lead to equations of the same form. This merely illustrates the well-known fact that identical quantitative relation systems may be developed from biologically different postulates, since these postulates are not, in their ontological significance, incorporated in the formulae.

In equations (19) and (20), s, $\left(\text{note that } \mu_t = \frac{p_t s}{n_t h}\right)$ is *number of eggs* distributed at random by each parasite: call this v. In equations (33) and (34) it is *fraction of area searched* at random by each parasite: call this w. Putting

$$n_t h e^{-p_t v/n_t h} = n_t h e^{-p_t w},$$

we get

$$\frac{v}{n_t h} = w.$$

When the values are such as to satisfy this equation, the values of n_{t+1} given by the two formulae will be the same. Taking v and w as values *to be calculated*, after initial numbers of hosts and parasites and effective reproductive rate of host have been determined, we see that for the steady state, or for the first generation in the unsteady state, it is not possible to decide whether parasites search areas at random, or search hosts at random.

Thus, suppose that we have an area of 100 sq. ft. containing 100 hosts, which produce in the next generation 200 hosts, so that the reproductive rate is 2. Suppose that in the first generation there were 10 parasites, and in the second generation 78·7 of the hosts are parasitized, so that 121·3 hosts emerge. If parasites search *areas* at random we have

$$121{\cdot}3 = 100 \times 2 \times e^{-10w},$$

$$w = 0{\cdot}05,$$

while if they search hosts at random, we have

$$121{\cdot}3 = 100 \times 2xe^{-10v/200},$$

$$v = 10.$$

An observation restricted to these facts, no matter how carefully conducted, therefore, would not enable us to decide which of the hypotheses is valid. If a parasite refuses to oviposit in the previously attacked hosts visited, so that only *one* egg is laid in any host, then there does not seem to be *any* way of distinguishing between the postulates, in the conditions stated. Again, if in the example previously given, each parasite, considered separately, searched 0·05 of the area and thus visits 0·05 of the 200 hosts in it, and deposits an egg at each visit, it will deposit 10 eggs and the 10 parasites will deposit 100 eggs. Thus even dissection of hosts will not enable us to distinguish between the two hypotheses in the conditions stated.

The study of animal interaction as a continuous process was initiated by A. J. Lotka. In 1923 Lotka made an analytical study of the qualitative relations between a population of host organisms and a parasite species preying on such a population. It appears, from his remarks, that the investigation was suggested to him by the original papers of the present writer in the *Comptes Rendus*, though he had studied a somewhat similar case in 1920. He objects to the formulation used on the ground that the time unit is virtually a generation, the limits of which, he thinks, "are, in the nature of things, ill-defined". If we consider the progeny of a thousand males born on 1 January 1900, says Lotka, "the births of their sons will stretch over a continuous period from about 1920 to 1950, the births of their grandsons from 1940 to 2000, their great-grandsons from 1960 to 2050 and so on. In a mixed population the limits of a generation are still more indefinite."

Following Lotka's later statement (1925, p. 88) and using the notation previously adopted, let n be the number of hosts, h, their birth-rate per head, (the deposition of an egg being counted as a birth), and d, their death-rate per

head from causes other than parasite attack. Let knp be the death-rate per head in the host population, due to invasion by the parasite, the coefficient k being, in general, a function of both n and p, the latter symbol designating the number of parasites. Suppose only one parasite develops in each host attacked. The total birth-rate in the parasite populations is then knp. If only a fraction k' of the eggs hatch, then the total birth-rate in the parasite population is evidently $kk'np$, which we may call Knp. Let the death-rate per head among the parasites be d_2. Then the rates of increase of host and parasite are given in the equations

$$\frac{dn}{dt} = (h_1 - d_1)\, n - knp, \quad \text{or,} \quad \text{putting } r_1 = h_1 - d_1,$$

$$\frac{dn}{dt} = (r_1 - kp)\, n, \tag{37}$$

and

$$\frac{dp}{dt} = (Kn - d_2)\, p. \tag{38}$$

It will be observed that r_1 is the *rate of increase* of the host and d_2 is the death-rate of the parasite; while k and K are coefficients on which depends the precise result of the encounters between host and parasite as affecting each of them, considered separately. The integration of these curves involves the elimination of t. The eventual result, to a first approximation, is a "family" of closed, asymmetrical curves, from which it appears that the sequence of events is cyclic or periodic. More exact treatment, according to this author, produces a spiral winding about a point of equilibrium, which may be interpreted as a diminishing or "damped" oscillation in time. Under the conditions stated, n will never fall to a zero value, i.e. the host will never be exterminated.

In 1926 Vito Volterra published his "Variazioni e fluttuazioni del numero d' individui in specie animali conviventi", inspired, as has been said, by discussions with the marine biologist, Umberto d'Ancona. After considering the case of a species living in isolation in constant conditions and of two species competing for the same food (a problem studied, as we have seen, by F. Muir (1914) for three species), he proceeds to consider that of two species, one feeding on the other. Suppose that if the birth-rate of the prey is α and its death-rate from causes other than the enemy is β, then the rate of increase will be $(\alpha - \beta) = \epsilon_1$. The death-rate of the predator, called by Volterra the coefficient of disappearance in the absence of the prey, being negative and written as $-\epsilon_2$, we may now say that ϵ_1 diminishes in proportion to N_2 (population of the predator), and to the extent $\gamma_1 N_2$, while $-\epsilon_2$ grows proportionately to N_1, and to the extent $\gamma_2 N_1$. The rates of increase of the two species will then be

$$\frac{dN_1}{dt} = (\epsilon_1 - \gamma_1 N_2)\, N_1, \tag{39}$$

$$\frac{dN_2}{dt} = (\gamma_2 N_1 - \epsilon_2)\, N_2. \tag{40}$$

We may note that the factors γ_1 and γ_2 are designated by Volterra as coefficients of defence and of attack, that

$$N_1=\frac{\epsilon_2}{\gamma_2}, \quad N_2=\frac{\epsilon_1}{\gamma_1} \tag{41}$$

are the equations of the "steady state", and that the co-ordinates of the equilibrium point in the cycle are the mean values of the number of individuals of the species during the cycle, so that, if γ_1, γ_2, ϵ_1 and ϵ_2 remain constant, the mean values of the individuals of the two species during a cycle will always be the same, whatever be the initial numbers of the individuals of these two species.

The equations of Volterra are thus identical with those of Lotka and constructed on exactly the same principles and postulates, though the methods adopted in solving them were quite different. Nevertheless, there is no doubt that Lotka's paper was entirely unknown to Volterra, who in 1927 publicly expressed his regret for his failure to cite his predecessor's paper.

As has already been said, equations for other types of animal interaction were produced by Volterra, and the work has been extended in many directions, both by this author and by Kostitzin (1934, 1937). However, it does not seem necessary to include these equations here. They cannot be integrated at present in any simple and convenient manner. The study of the hypotheses in various numerical settings is therefore difficult, and though the expert can sometimes indicate the general form of the solutions, the biologist does not usually possess a mathematical equipment sufficient for this.

It is, however, interesting to consider briefly the postulates utilized by Lotka and Volterra, since the value of the system, as a representation of natural phenomena, ultimately depends on them.

The first postulate, which is required for the use of the differential calculus, is that the group of individuals constituting the population concerned can be represented by any positive number, varying with time in a continuous manner; so that we can legitimately postulate an infinitesimal increment or decrement of the population for an infinitesimal increment of time.

The fact that this postulate is essential for the use of the differential calculus does not mean that it is biologically acceptable. Reproduction doubtless occurs practically continuously in large human populations, but in many organisms it is definitely periodic, and though the generations may overlap because parents live to reproduce at the same time as their offspring, the generation times have definite limits. Moreover, many species, and vast numbers of insects, particularly, have only one or two generations a year and do not survive the reproductive period.

We have shown elsewhere (1931*b*, pp. 154, 155) that even with organisms with overlapping generations, the compound interest law in its simple form does not correspond to the facts, at least under conditions where experimental or field studies are possible. Generally speaking, the phenomena as they occur

in nature are essentially discontinuous. The populations are whole numbers, which change by finite increments and decrements, while the generations require finite periods of time and are distinct and discrete. When cyclical changes occur in nature, as they sometimes do, the generation periods are usually very large in relation to the period of the cycle. The cycles do not occur in such a way that we can legitimately relate an infinitesimal increment or decrement of population to an infinitesimal increment or decrement of time. It seems, therefore, that the methods of the infinitesimal calculus are not really suitable for studying the changes in real populations and that there is no way of eliminating this difficulty.

The second fundamental assumption is that encounters of host and parasite are entirely random. This is implied by the statement that the frequency of encounters is a simple function of their numbers. We have already set out in detail the reasons for rejecting this assumption.

Finally, the increase and decrease of the populations concerned is, in this theory, *entirely dependent on their encounters with each other, as predator and prey*. This assumption is evidently false, since the effective reproductive rate depends not only on *this* encounter, but on all the other innumerable encounters with environments that occur during the course of the life history. The causes of mortality are radically multiple, the values of the coefficients of attack and defence are radically inconstant. Since it is impossible to connect up the incidents forming the material of this theory without interpolating a multitude of others which it does not and cannot embrace, the deductions concerning the variations in animal members derived from it, cannot be regarded as applicable to the changes in natural populations.

E. Cameron, in the concluding pages of his recent study of the natural control of the pea moth (*Cydia nigricana* Steph.) (1938), has clearly shown how the conditions produced by the normal practice of crop rotation make an application of mathematical methods to the generation sequences of many agricultural pests almost unthinkable. Kostitzin (1934, 1937), though an active worker in this field, has admitted that very serious objections can be made against the idea that the "vital coefficients" are constant, as the theory requires.

The fact that experiments carried out with certain Protozoa by Gause have given curves similar to those derived from the Lotka-Volterra equations (cf. Gause, 1934, ch. VI), has been described by Volterra & d'Ancona as "a very important experimental verification of the mathematical calculations" (1935, p. 89). But in the first place, even under experimental conditions, Gause did not obtain continuous periodic fluctuations of the type given by the equations. In the most striking of his experiments (*Paramoecium* v. *Didinium*) the predator invariably annihilated the prey and then died out itself; while in the experiments giving results in conformity with theory, these were secured by artifices, such as the very crude artifice of adding to one of the populations. It would not be surprising to find that under certain experimental conditions

and with certain particular species, events occur according to the law of the equations. Such results would not, however, justify us in accepting these equations as the basis of a theory of natural populations, for the reasons already given.

Bailey and Nicholson (1931, 1933, 1935) have made several objections to the formulation proposed by Volterra. The improvements they have actually made appear, as has been said, to depend mainly on the advantages naturally derived from the simple discontinuous system utilized, since their efforts to obtain the solutions of an adequate continuous function system have been unsuccessful.

On the other hand, as the examples given show, the equations in the discontinuous system are relatively easy to construct and manipulate. They offer a very convenient method of investigating certain of the postulates of Lotka and Volterra numerically, as Nicholson & Bailey have shown. Though the formulations are not identical, the fundamental postulate of random searching of environments can be incorporated in the two systems, so that they lead to similar results. Thus, the equations of Volterra for predator and prey give for certain values of the constants a series of oscillations of host and parasite of identical form, perpetually recurring; the discontinuous equations give, in some cases, a series of similar oscillations, though these increase in magnitude, so that eventually the value of n_{t+1} falls below unity, which may be interpreted as indicating the extermination of the host, followed by that of the parasite. Nicholson & Bailey say that the departure from the steady state sets up a reaction "tending to cause a return to this density"; but this "tendency" never attains the end to which it is supposed to be directed. The oscillations become *more*, not *less* violent.

Volterra's equations are very difficult to deal with, but the interesting consequences that follow from strict dependence of parasite reproductive rate on host density can be readily worked out in the discontinuous system. For example, Nicholson & Bailey show that if we have a parasite reproducing simultaneously in two hosts, of which one, having the population k, is unaffected in its density by the attack, while the other varies in number under the influence of the parasite, whose population in each generation breeds up on the *two* hosts, the situation of the second host and its parasite may be represented by the equations

$$n_{t+1} = n_t h e^{-p_t s}, \tag{42}$$

$$\begin{aligned} p_{t+1} &= n_t h\,(1-e^{-p_t s}) + k\,(1-e^{-p_t s}) \\ &= (n_t h + k)\,(1-e^{-p_t s}), \end{aligned} \tag{43}$$

supposing the parasite has the same "area of discovery" for the two species. Under these conditions the values for n_{t+1} form a damped oscillation (Nicholson & Bailey, 1935, Fig. 14).

The mathematical results derived from the postulate that the environments are searched at random are thus rather more attractive, from the aesthetic standpoint, than those following from the postulates of non-random searching.

or random choice of hosts. They are, for that reason, stimulating to the experimenter. Unfortunately, for the very same reason, the hypothesis is more vulnerable if considered in relation to events in nature, because variations in the value of the *area of discovery*, added to variations in the reproductive rate of the host insect, destroy the delicate relationship which is the basis of the pleasing curves obtained in the random contact system. The hypotheses leading to forms of simple geometrical progression have, artistically, less to lose, and do not suffer quite so severely when the postulate of constancy has to be abandoned.

On the other hand, it should be clear, from what has been said, that none of the multitude of mathematical relation systems that can be constructed by altering the fundamental postulates and combining them in various ways can be taken as a basis for deductions that will tell us what is really happening in nature. The simple truth about the mathematical theories is that they are mathematical, and not biological. Dressing them up in biological language may conceal this fact, but does not alter it.

Studying the equations for the "steady state" or the "parasitic cycle" is, in fact, exactly like studying the mathematical definitions of the sphere or the triangle. If we accept the Euclidean axioms, we can deduce from the definitions of the triangle the fact that the sum of its interior angles is equal to two right angles. This truth is implicit in the definition of the Euclidean triangle. It is not necessary to draw triangles on paper and carry out microscopic measurements, in order to demonstrate it. On the other hand, the fact that inevitable inaccuracies in construction and measurement prevent us from giving a demonstration that is at once practical and absolute, does not in the least invalidate the Euclidean proposition. If a perfect Euclidean triangle exists in nature, the sum of its interior angles will quite certainly be equal to two right angles.

For the same reasons, we can say, without fear of contradiction, that if we have a situation in nature fully and accurately described by the equations of the "steady state", we may be sure that the numerical values involved will be as they are in the equations. If the value corresponding to one symbol is altered, and the value of the expression remains the same, the value corresponding to some other symbol must have altered, in the manner required by the expression. This is simply equivalent to saying that if a triangle exists in nature it has the properties of a triangle. To talk about "verifying" propositions of this kind by observation is meaningless. The same thing is true for the equations of the parasitic cycle. If all the quantities follow the law of the equations, the progress of events will be as specified in the equations; it cannot be otherwise. But it must be noted that these equations contain t which is the symbol for *time*, which depends on the change in real things, to discover which we must look at real things; so that the equations containing t, while more interesting than the others, are more insidiously deceptive; more likely to make us think that we can know in advance, things we have still to find out.

During the course of his mathematical experiments, the writer drew a good many deductions concerning practical operations and the sequence of phenomena in nature. In one paper (1927*a*) he attempted to show how the methods developed could be used, in calculating the progress of introduced parasites in the field, and predicting the date of control. Unfortunately, the results of field studies do not give much ground for the hope that the mathematical treatment will be of great practical value, no matter how it is modified. The difficulty, as has been said, is that the values assumed in the formulae to be constants are not constants in nature. The writer tried to get round this difficulty by arguing that irregularity produced by environmental conditions *will average out in time* (1930*b*, p. 648). This argument was based on the fact that when climatic factors, such as rainfall and temperature, have been averaged for a period of say 50 years, a figure is obtained from which the average subsequent periods will not notably deviate. But further reflexion has shown the writer that this has little bearing on the point at issue. The effect of the variation in climatic factors will almost certainly be a variation in the reproductive rates of host and parasite. The result will be that the sequence of events, instead of being that of equations (1) and (2) for example, will be

$$n_t = n\,(h, i, j, k \ldots \text{to } t \text{ factors}) - pa\,(h, i, j, \ldots, \text{to } (t-1) \text{ factors}) - pab\,(h, i, j, \ldots, \text{to } (t-2) \text{ factors} - pabc\,(h, i, j, \ldots, \text{to } (t-3) \text{ factors}, \ldots, \text{etc., all to } (t+1) \text{ terms}),$$

$$p_t = p\,(abc \ldots \text{to } t \text{ factors}).$$

These are not geometrical series and cannot be summed. Moreover, there is no reason to think the values $h, i, j, k, \ldots$ and $a, b, c, \ldots$ follow each other according to any particular law. If they do, we do not know what the law is. In short, it is clear that the most important assumption underlying the mathematical formulation is incorrect and that we have at present no way of rectifying it.

It is difficult and indeed unwise to set any limits to the usefulness and practical application of mathematics and especially of an instrument as powerful as the infinitesimal calculus; but so far as the writer can see, there is, in the last analysis, no way of developing a method that can reduce to manageable form the appalling complexity of natural factors or smooth out their unpredictable irregularities. When the mathematicians can produce a system enabling us to predict the climatic conditions next year, next week, or even to-morrow, and reduce their fluctuations to mathematical laws, we may begin to talk about mathematical theories of natural populations. It does not seem that they are likely to do this very soon.

VI. CONCLUSIONS

The task of the economic biologist is the production and maintenance of a relation advantageous to man, between the beneficial and noxious organisms in the environment. His problem is therefore a problem of populations

considered particularly from the quantitative standpoint. As we have shown, economic entomologists in general and students of biological control especially have for many decades interested themselves in population problems, though their work has, until recently, attracted relatively little attention from academic workers in this field.

During the past ten or fifteen years biologists and mathematicians have, however, come to realize the great interest and importance of population studies, and a great research movement is rapidly developing. A good deal of the investigation that is in progress consists simply in the extension with improved methods, of the field work that constitutes the normal programme of the economic biologist. But much of it has now to do with the mathematical theory of the interaction of organisms. This has been very rapidly developed and extended. As Salt (1932, p. 211) has justly remarked, "theory...has far outstripped experiment".

Nevertheless, though the experimental work inspired by the theory is still in its initial stages, and has not, in spite of the too optimistic assertions of some authors (e.g. Volterra & d'Ancona, 1935, p. 90) given results that can be considered as genuine verifications, yet the mathematical construction is so elegant and impressive that there is already a tendency to overestimate its value and to offer it as a description of what really happens in nature, from which, therefore, we can safely deduce rules for practical operations. Thus Volterra himself (1937, p. 330) has recently said that in biological control work these population theories play a part of the first importance.

Now it is quite true that some of the work in biological control is ordinarily carried out on empirical lines and that everyone engaged in it would like to put it on a really scientific basis. But, after all, "empirical" is simply another word for "experimental", and in entomology, which is an inductive science, experiment and observation are the proper methods of getting the facts.

Suppose we intend to introduce a certain number of parasitic insects, belonging to some particular species, into the Dominion of New Zealand to combat a pest of cabbages. We might discover in advance what will happen, by a deduction from mathematical premises, provided those premises were correct. But we do not know that the premises of our mathematical theories *are* correct; particularly as applied to conditions in New Zealand. We must therefore verify them. But this is an extremely difficult, complex and laborious task; and even when we have completed it to the best of our ability, we cannot be sure that the results are correct. The verification must itself be verified, and the only way of doing this is to introduce the parasites into New Zealand and observe the results. On the whole, therefore, it seems simpler and more satisfactory to do this in the first place; and that is what is usually done.

This does not mean that operations in biological control are carried out in an unscientific manner. On the contrary, these operations and the technique connected with them have become steadily more scientific. Field surveys, the study of parasite biology, the work of collection, shipment, breeding and

liberation, the investigation of results in the field, have now been organized, on the basis of experimental work carried out in the past, so that the desired results can be obtained with relative certainty and accuracy. We may say that in these departments we already possess a collection of scientific principles, on which our work is based.

Furthermore, we also possess a theory of organic populations and natural control, built on the study of events as they occur under natural conditions. This theory, which has been outlined in preceding sections of this paper, is biological, not mathematical. It is, indeed, rather a statement of fact than a theory. It enables us to understand, in a general way, how outbreaks of pests arise and why they come to an end; and how organisms of different kinds can exist together in nature. It does not give any ground for thinking that the numerical changes in populations follow any simple and uniform law which could be represented by a mathematical equation. It indicates, rather, that natural control works in a way that normally excludes the possibility of such laws. It is evident that if the situation in nature corresponded exactly to the mathematical equation, the laws inherent in the equation would be the laws of nature; just as the mathematical relations of surface and radius in a billiard ball are (or might be) those given by the equation of the sphere. But conditions in nature clearly do not reproduce the conditions in the equations, because of the tremendous complexity and irregularity of natural phenomena; and it is useless and worse than useless to pretend that they do, because the investigator labouring under this delusion may be tempted to force the facts into a mould that will not fit them or may try to find the facts, not in nature, but in the mathematical representation of nature that he has himself constructed.

This is not to say that the mathematical theories of populations are useless. They enable us to see clearly how one quantity varies in function of others, under certain definite conditions. They may suggest and have already suggested experimental investigations and field studies from which very valuable information is derived. But they do not, and cannot, provide rules for practical operations, and they are not in any degree a substitute for the investigation of nature.

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FIELD STUDIES ON COCCIDIOSIS IN THE RING-NECK PHEASANTS OF EASTERN WASHINGTON

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(With Plate XI, containing Figs. 1–13)

CONTENTS

		PAGE
I.	Introduction	389
II.	Material and methods	390
III.	Taxonomy	391
IV.	Incidence of infection	393
V.	Histopathology	394
VI.	The effect of temperature on development	395
VII.	Discussion	396
VIII.	Summary	397
	References	398

I. Introduction

Very little has been accomplished in the way of actual field studies on coccidiosis in game birds or animals. Records of any systematic survey of game birds for this particular disease are very few and, so far as can be ascertained, no field surveys of coccidiosis in the ring-neck pheasant have been made. In most cases the presence of coccidiosis is noted with very little information as to incidence, distribution, damage to the birds, or identity of the species of coccidia involved.

Tyzzer's (1929) is the only work on the coccidia of the ring-neck pheasant that has been published in this country. He described, in the eastern United States, two new species of *Eimeria* from the pheasant. They were *E. phasiani* and *E. dispersa*, the last of which he also found in the Virginia quail, *Calinus virginianus*.

The term coccidiosis is used here as indicating the presence and multiplication of either pathogenic or innocuous coccidia within the host.

Coccidiosis in pheasants has also been reported by Fantham (1910) in Great Britain and by Hadley (1910) in the United States. The latter author classed the pheasant coccidia he found under the name *Eimeria avium*. This name was used loosely, prior to 1915, to include the *Eimeria* found in a number of different birds. It is no longer used as a species name for any of the *Eimeria* from pheasants. Henry (1931*a*), in examining quail (*Lophortyx californica* and *Oreortyx picta plumifera*), failed to find *Eimeria dispersa* in California.

The purpose of this paper is to report observations on (1) the distribution and incidence of coccidiosis in the ring-neck pheasant in Whitman County, Washington; (2) the damage caused by the disease and some of its histopathology; and (3) the result of morphological and biological studies which were made to determine what species of *Eimeria* were present.

The so-called ring-neck pheasant is a hybrid that has been introduced into this country. It is a cross between *Phasianus colchicus torquatus* and *P. c. colchicus* according to Leffingwell (1928).

II. Material and methods

The pheasants were procured during and after the hunting season. They were shot and the material taken from them within 1–4 hr. The faecal material was taken from both the caeca and the lower intestine and immediately examined microscopically for the presence of oocysts. If oocysts were not found some of the material was subjected to the following standard flotation method in order to concentrate the oocysts if present, and to ascertain the relative severity of the infection. Faecal material, to the amount found in a normal dropping, which had been mixed with 15 c.c. of 2 % $K_2Cr_2O_7$, was again thoroughly mixed by agitation and 3 c.c. put in a centrifuge tube. Twice that volume of saturated NaCl solution was then added and mixed with the faecal material. The mixture was then centrifuged in a hand centrifuge for 3–5 min., allowed to stand for 5–10 min., and a loopful put in a hanging-drop slide. The presence of under 100 oocysts in 1 drop was considered to be indicative of a light infection. A heavy infection was considered to be one comparable to a heavy chicken infection in which gross lesions or some inflammation of the gut combined with an oocyst count of over 100 would be found. No heavy infections were encountered.

I found the following modification of the standard technique for preparation of stock cultures more satisfactory for the light infections encountered. A 2 % $K_2Cr_2O_7$ solution was mixed with the undiluted faecal material and the mixture stored at 20° C. No appreciable difference in developmental times was noted between the oocysts in the stock culture of the faecal material and those transferred to normal physiological saline which was practically bacteria free. A concentration greater than 2 % of $K_2Cr_2O_7$ was apparently injurious to the oocysts in some cases, although a 2·5 % solution is recommended by workers in the field for other *Eimeria*. Becker (1934) has stated that it was advisable to separate the oocysts from most of the bacteria by dilution and centrifugation, but it was not found that failure to do this resulted in any untoward effects on the oocysts. Storing the undiluted faecal material directly with $K_2Cr_2O_7$ also had the advantage of reducing handling of the material and possible injury to the oocysts. Storage of the oocysts in undiluted faecal material alone inhibited development completely.

In other work upon "sporulation times" and development of oocysts, it is

usually stated that room temperature was used. Since room temperature may vary considerably, all cultures were incubated at 20° C. for purposes of future accurate comparison.

For purposes of study the oocysts were concentrated by means of flotation in saturated salt solution and put in hanging drops. They were then transferred to hanging drops of physiological salt solution which were sealed in depression slides. Transfers were accomplished by means of the Chambers micropipette (Chambers, 1923). The change to physiological saline was found to be necessary, since many of the oocysts would collapse if left in saturated salt solution.

Segregation by means of the micropipette was found to be comparatively swift and easy, and had a further advantage in that oocysts of the different species could be segregated from mixed infections and their development checked more easily and certainly than if they had been left in the mixed culture. Incidentally this method of culturing oocysts cuts down greatly the number of bacteria present as is recommended by Becker (1934).

The intestine was examined for gross lesions, and pieces of the intestine were taken from various regions and fixed in Zenker's or Bouin's fixative. Sections 6μ thick were stained with Harris haematoxylin, counter-stained with eosin and mounted in balsam for examination of the endogenous forms of the parasite. Tissues were taken from the intestine and the caeca at various measured localities in each case.

Temperature experiments on the living oocysts were carried out in thermostatically controlled constant temperature cabinets. The oocysts were contained in hanging drops of physiological saline (0·85 %) solution. Evaporation of the hanging drops was prevented by placing slides in Petri dishes containing moistened filter paper and sealing the Petri dishes with rubber seals.

The term "sporulation time" used in the following sections is taken to mean the time between extrusion of the oocysts in the faecal material and the formation of sporozoites within the sporocysts.

III. TAXONOMY

Three and possibly four species of *Eimeria* were found to be present in the Chinese pheasants of Whitman County.

Eimeria phasiani Tyzzer, 1929

Figs. 6, 9

Individuals of this species corresponded closely to the descriptions given by Tyzzer. They averaged slightly larger in size as can be seen in Table I. The oocyst wall was 2μ thick, a light yellowish brown in colour, and was composed of two cyst membranes. The contour of the cyst was smooth.

Oocysts of *E. phasiani* were in pure culture in four of the pheasants examined. The unsegmented cell of the oocyst is fairly smooth in outline and

Table I. *Comparison of the species of* Eimeria *found in the ring-neck pheasant*

	*E. phasiani**	*E. phasiani*	*E. pacifica*	*E. megalostomata*	Type IV
Length	23 μ	25 (21–27) μ	22 (26–17) μ	24 (21–29) μ	18
Width	15·9 μ	17 (15–19) μ	18 (20–14) μ	19 (16–22) μ	15
Index	0·69 μ	0·71	0·81	0·79	0·83
Shape	Ellipsoidal	Ellipsoidal	Ovoidal	Ovoidal	Ovoidal
Thickness cyst wall	—	2 μ	1·8 μ	2 μ	2·2 μ
Membranes present	—	2	2	3	—
Polar inclusions	1 or more refractile	2–3 refractile	2–3 refractile	1, dark and irregular	1 refractile
Sporulation time	24 hr. at room temp.	24–36 hr. at 20° C.	48 hr. at 20° C.	48 hr. at 20° C.	—
Micropyle	None	None	None	Present	None

* Data given by Tyzzer (1929).

touches both sides of the oocyst wall. The sporoblasts are at first rounded in form (Fig. 8), but later elongate to form the sporocyst seen in Fig. 9. One or two small dark residual granules can sometimes be observed. The inner membrane is closely applied to the outer and could be seen as a very thin colourless layer in oocysts that had partially collapsed due to their continued immersion in saturated salt solution.

Fifty specimens were measured to obtain the dimensions given.

Eimeria pacifica n.sp.

Figs. 10–13

Diagnosis. Length 22 μ (26–17); width 18 μ (20–14); index, width to length, 0·81; shape ovoid; contour smooth; colour light yellowish; thickness of cyst wall 1·8 μ; two cyst membranes present; two or three refractile polar inclusions; sporulation time 48 hr.

Oocysts of *E. pacifica* were identified in four of the pheasants examined and obtained pure culture in one of them. The unsegmented cell of the oocyst is somewhat irregular in outline and usually touches both sides of the oocyst wall.

Several small residual granules are sometimes seen. The sporocysts are elongate and pointed at one end.

The inner membrane lies very close to the thick brown outer envelope and can be observed only in partially collapsed oocysts.

Fifty specimens were measured to obtain the average dimensions given above.

Eimeria megalostomata n.sp.

Figs. 3–5

Diagnosis. Length 24 μ (21–29); width 19 μ (16–22); index, width to length, 0·79; shape ovoid; contour smooth; colour light yellowish brown; thickness of cyst wall 2 μ; three cyst membranes present; one dark, irregular polar inclusion; sporulation time 48 hr.; micropyle present.

Oocysts of *E. megalostomata* were obtained from two of the pheasants examined. They were in mixed cultures with *E. pacifica* in both birds.

The unsegmented oocyst is smooth in outline and almost fills the cyst cavity (Fig. 3). The outline of the cyst is more rounded than that of *E. phasiani* or *E. pacifica*, and is remarkable because of the large micropyle (Fig. 3) which is apparent.

The sporoblasts are rounded at first, but later form elongate sporocysts that are pointed at one end.

No residual granules are present.

This species has three membranes that can be seen in the region of the micropyle. There is a very thin, colourless, outer membrane, a thick, yellowish brown, middle membrane and a fine, colourless inner membrane.

There is one large, dark, irregularly shaped polar inclusion present which is usually directly in front of the micropyle.

Thirty specimens were measured to obtain the average dimensions given.

Type IV

In addition to the three above mentioned types, there were found three small oocysts, already segmented, in a culture of *E. phasiani*. They were clearly different from the others. They averaged 15μ in width by 18μ in length, with a width to length index of 0·83. They were further distinguished by the presence of but one refractile polar granule and by a slightly thicker, yellowish brown cyst wall.

These oocysts may have been aberrant specimens but the similarity of their appearance and size would seem to indicate the possibility of still a fourth type of *Eimeria* being present in pheasants. In the comparative chart, Table I, they are designated as type IV.

IV. INCIDENCE OF INFECTION

Most of the pheasants were collected along the upper half of Union Flat Creek, Whitman County, Washington. In the fall they were found scattered out in the wheat fields surrounding the creek. In the winter they were concentrated in the brush along the creek bottom. No significant localization in the distribution of the infected birds was found.

There were several interesting seasonal changes in the incidence of coccidiosis which are shown in Table II.

A total average incidence of 38 % was found in the pheasants examined. This includes all species of *Eimeria* found. Table II indicates the source of the statistics given. The relative number of birds examined was small and does not permit conclusive statements to be drawn. It is, however, indicative of trends in the incidence of the disease.

Table II. *The monthly incidence of coccidiosis*

Birds collected	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Uninfected	3	6	—	2	5	5	1
Infected	7	2	—	0	2	2	2
Total	10	8	—	2	7	7	3

V. Histopathology

The histopathological studies were made entirely on the tissues of adult birds which had become naturally infected. All the tissues, therefore, are presumed to be from chronic or partly immunized cases.

Macroscopic lesions in these naturally infected birds were almost entirely lacking. In one infection of *E. pacifica*, and in a mixed infection of *E. megalostomata* and *E. pacifica*, there was slight external inflammation of the gut in the region of the upper intestine.

In pure *E. pacifica* infections the endogenous forms appeared equally numerous throughout the upper intestine and the caeca. Infection in the caeca was extremely light in all specimens examined. Just an occasional cell contained a parasite. In no case did there appear to be any extensive damage to the epithelium as a whole.

The schizonts observed in pure infections of *E. pacifica* (see Figs. 1, 2) were situated both above and below the nuclei of the epithelial cells and had caused no enlargement or ballooning of the cells as noted by Tyzzer (1929) in *E. phasiani*. This furnishes additional proof of the validity of *E. pacifica* as a distinct species. The schizonts seen had deeply staining slightly irregular nuclei and very light staining clear cytoplasm surrounded by a fine cell membrane. This could not always be clearly seen.

In tissues of a bird infected by *E. megalostomata* and *E. pacifica*, macrogametes in various stages were found in the cells of the villi of the upper intestine. They were above the nuclei of their respective cells and appeared to be in the process of being extruded from the epithelial lining by rupture of the cells in which they were contained. There was no such development beneath the epithelium such as Tyzzer observed in *E. maxima* and *E. tenella* of the chicken. It cannot be known for certain whether these were macrogametes of *E. megalostomata* or *E. pacifica*. Schizonts in stages similar to those formed in the pure *E. megalostomata* infections were also found. They exhibited no differences from the schizonts formed in pure *E. pacifica* infections.

The distribution of the organisms in the intestine was the same for the birds infected with *E. megalostomata* and *E. pacifica* as for those infected with only *E. pacifica*. In both cases there was very little attack on the epithelium of the caeca while the upper intestine seemed to be evenly infected throughout its length. The *E. pacifica* infection combined with that of *E. megalostomata* would probably tend to mask the true distribution of *E. megalostomata*, especially in such light infections and where there appears to be no great difference between the intracellular forms of the two species.

VI. THE EFFECT OF TEMPERATURE ON DEVELOPMENT

There was a noticeable difference in the rate of development in oocysts kept at 20° C. and at room temperature which varied several degrees during a 24 hr. period. In one lot of oocysts of *E. pacifica*, part of which were left at room temperature, and part of which were maintained at 20° C., partial or complete sporulation was observed at 28 hr. in thirty-five out of forty-five oocysts left at room temperature, while no cleavage or indication of it could be observed in the oocysts maintained at 20° C. until more than 8 hr. later.

Viable oocysts of *Eimeria pacifica* were subjected to a range of temperatures from 0 to 37·5° C., and their developmental times were checked. The optimum temperature for development in these experiments was 30·5° C. At that temperature sporulation was complete at 20 hr. *E. perforans* of the rabbit completes sporulation most quickly at temperatures between 25 and 38° C. according to Perard (1925). Nohmi (1926) reports 30° C. as the optimum temperature for sporulation of *E. zurnii* of the ox.

At 37·5° C. no change took place up to 149 hr. in *E. pacifica*. Then the large dark granules that are scattered through the cytoplasm in the normal undeveloped oocyst had migrated to the periphery of the cytoplasmic mass where they formed an irregular dark border. At 227 hr. degenerative changes were setting in. A small refractile globule became apparent in the cytoplasm. The protoplasmic mass gradually shrank to one-half its original size. When put at 30·5° C. at 275 hr. it showed no change and was quite evidently dead. Fish (1932) in his work on *Eimeria tenella* of the chicken gave 51·5° C. for 10 min. as a lethal temperature. His experiments were performed using a 2·5 % solution of $K_2Cr_2O_7$ and are open to the criticism that $K_2Cr_2O_7$ at that temperature might be partially responsible for the death of the oocysts. Perard gives 40° C. as being lethal for *E. perforans* within 24 hr.

There was no apparent difference in developmental times between the temperatures of 15 and 28° C. in *E. pacifica*. Sporulation was complete at 48 hr. in oocysts kept at 28, 21 and 15° C. respectively. Perard found that at 18° C. sporulation occurred at 48 hr., but that at 25° C. the developmental time was cut to 30 hr. in *E. perforans*.

In oocysts of *E. pacifica* kept at 8° C. there was no segmentation up to 275 hr. The only change was the migration of the large dark granules (Fig. 11) to the periphery of the cell where they formed a slightly irregular dark border similar to that formed in the oocysts kept at 37·5° C. At 275 hr. the oocysts were transferred to 30·5° C., whereupon sporulation occurred within 18 hr. The first observation was made 18 hr. after they had been placed at 30·5° C. and sporulation had already been completed. This would seem to indicate definitely a certain amount of intracellular organization prior to segmentation. It may be that if oocysts were left long enough at 8° C. that they would eventually sporulate. Perard found that *E. perforans* completed sporulation in 2 weeks at 5–6° C. Nohmi (1926) reported that *E. zurnii* of the ox did not sporulate at 11–15° C. within 15 days.

In oocysts placed at 0° C. no change was noticed except the same migration of the large granules to the periphery of the cell where they formed a dark border similar to the one observed in the oocysts kept at 8 and 37·5° C. At 275 hr. they were placed at 30·5° C. and their development observed. Segmentation did not occur before 36 hr., although a small polar body did appear at 18 hr. in one of the oocysts. This might be interpreted as indicating that the oocyst could not possibly eventually sporulate at 0° C., since no intracellular preparation for sporulation could be observed, as evidenced by the rate of development after being placed at the optimum temperature. Perard found that *E. perforans* underwent no development in a watery medium at 0° C. also.

VII. Discussion

Maintenance of the infection in nature may be accomplished by any or all of several different combinations of circumstances.

Tyzzer (1932) states that preliminary experiments in his laboratories tended to show that oocysts died rather quickly when exposed in the soil. Chickens were put in runs occupied by infected flocks 50 days previously, and failed to contract the disease. Delaplane & Stuart (1935) in Rhode Island have shown, however, that oocysts of *E. tenella* survived in plot soil through the winter and spring for 4–9 months after the removal of infected fowl from the plots. The soil of a wooded range in their experiment showed viable oocysts at 15 and 18 months after the removal of all fowls from it.

Van Es & Olney (1935) in Nebraska demonstrated coccidial infection from pens previously unoccupied for 5 months. My experiments with the effects of different temperatures on the oocysts indicate that they can live for at least 15 days at temperatures as low as 0° C. and still be able to develop normally if the temperature rises to or above 15° C., and that they will develop normally in temperatures up to 30·5° C. This means that they could live in the soil and develop to the infective stage during most of the year provided that the moisture in the soil remained sufficient to prevent desiccation.

The experiments quoted, with the exception of the preliminary work of Tyzzer, show that infection in the pheasants may be accounted for by the survival of oocysts in soil or through the existence of carriers which might continually cause infections in other birds by faecal contamination. Combine this work with the work of Tyzzer (1932), Hall (1934) and Becker (1934), which show that one oocyst may be an infective dose, and the possibilities for pheasant infection by contact with contaminated soil becomes apparent. This would be especially likely when they are gathered in coveys in the summer and fall, or concentrated into protected areas during the winter. The possibility of carriers existing becomes remote when the behaviour of the endogenous stages in the epithelial cells is considered. The tendency in infections of all the pheasant coccidia studied is for the oocysts to be extruded from the infected cells into the lumen of the gut. Carriers have so far been demonstrated (Herrick *et al.*

1936) only in *E. tenella* infections in chickens where the infected epithelial cells become trapped in the submucosa.

In all the infected birds examined the infection had caused only slight damage. The number of oocysts thrown off was small, there was little damage to the epithelium and the weights of the infected birds compared very favourably with those of the uninfected. On the other hand, it must be realized that fatal cases in wild birds would be very hard to trace since predators and scavengers of several kinds are constantly on the alert for dead or weakened birds. Also, the most likely place to look for acute effects is in the young birds.

Stoddard (1932) states that coccidiosis is believed to be an important factor in the mortality of young quail. This is pertinent information since the quail and the pheasant have in common certain habits of flocking together, of raising large families, and of spending a great deal of time on the ground.

The fact that the infections found in the pheasant in October were uniformly light is suggestive of a heavy infection among non-immunes having appeared sometime earlier in the summer. The heavy spring infection would have been in the young birds since the older ones would probably possess partial immunity.

This would have come about in the following manner. Around 80 % of the pheasant population is killed every year by hunters and replaced by young birds. This provides a large susceptible population. Oocysts coming from the older birds would cause widespread infection in the younger ones. These new cases would be either recovered or dead by the end of August, since the main hatch of pheasants is in June, and the primary infection, if it is comparable to similar infections in chickens (Tyzzer, 1932), probably does not run for over a month. Reinfection that occurs in the late summer or fall does not take an acute form as is evidenced by post mortem examinations. As soon as the coveys are broken up by the hunters the opportunity for continued reinfection is decreased and the incidence of the disease drops sharply.

It is not yet proved that any of the species of *Eimeria* observed give rise to fatal or even acute cases of coccidiosis. Further epidemiological field studies should be made with particular attention being paid to the effect of the disease in the young birds.

VIII. SUMMARY

1. An average incidence of infection of 38 % was found in thirty-seven ring-neck pheasants over a period of 7 months.

2. There was a drop in the incidence from 70 % in October to 30 % in November. The incidence remained at 30 % during February and March and jumped to 67 % in April.

3. Three species of *Eimeria* were identified: *E. phasiani* Tyzzer and two new species, *E. pacifica* and *E. megalostomata*. A fourth type designated as type IV was seen but not described because of an insufficiency of specimens.

4. All infections observed were light. Histopathological studies showed little damage to the intestine and there was no significant difference between the weights of infected and non-infected birds.

5. Oocysts of *E. pacifica* sporulated at temperatures from 8 to 30·5° C. The latter is the optimum temperature. Intracellular organization prior to sporulation was indicated in oocysts of *E. pacifica* kept at 8° C.

6. A temperature of 37·5° C. was lethal to oocysts of *E. pacifica*. Degenerative changes in the oocysts were first observed 9 days after being placed at that temperature.

This work was done in the Zoology laboratory of Washington State College, Pullman, Washington. I wish to acknowledge my indebtedness to Dr R. F. MacLennan, of that Institution, for suggesting the problem, for his help and co-operation in the prosecution of the work, and to Dr F. S. Henika for assistance in the collection of specimens. I also wish to acknowledge my indebtedness to Dr Victor Burke and the Dairy Department for the use of the apparatus. Acknowledgement is also made to the Washington State Department of Game for permission to collect pheasants.

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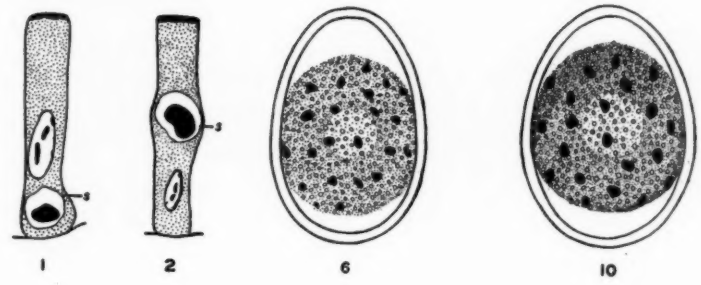

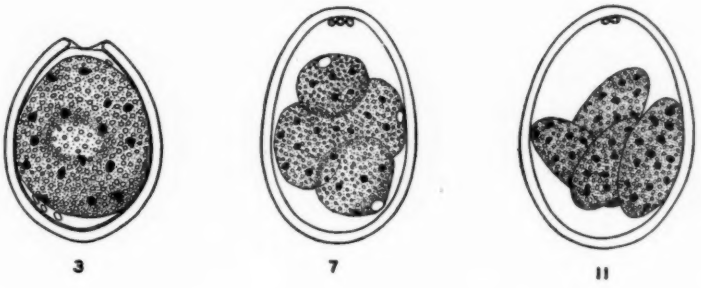

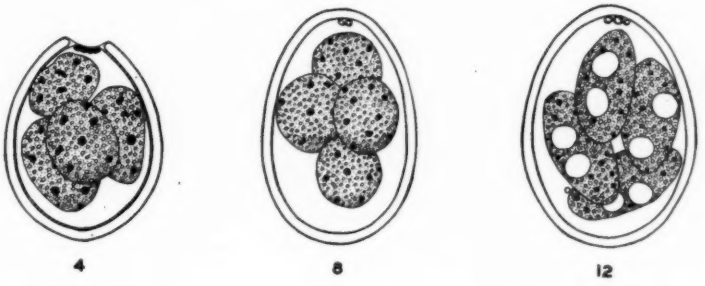

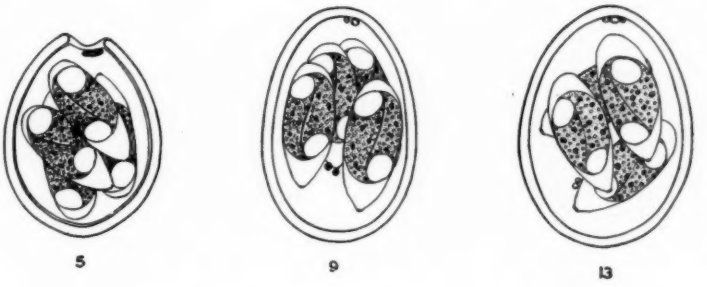

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EXPLANATION OF PLATE XI

Fig. 1. A schizont of *E. pacifica*.
Fig. 2. A schizont of *E. pacifica*.
Fig. 3. An undeveloped oocyst of *E. megalostomata*.
Fig. 4. The developing oocyst of *E. megalostomata*.
Fig. 5. The mature oocyst of *E. megalostomata*.
Fig. 6. The oocyst of *E. phasiani* prior to any development.
Fig. 7. Developing oocyst of *E. phasiani*.
Fig. 8. Developing oocyst of *E. phasiani*.
Fig. 9. Mature oocyst of *E. phasiani*.
Fig. 10. An unsegmented oocyst of *E. pacifica*.
Fig. 11. Maturing oocyst of *E. pacifica*.
Fig. 12. Maturing oocyst of *E. pacifica*.
Fig. 13. Mature oocyst of *E. pacifica*.

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